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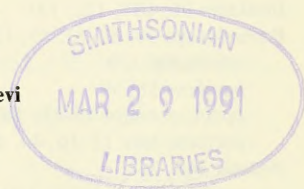
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(Compiled by Tomio Iwamoto)

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Blakea fuchsioides
Blakea gregii
Blakea hammelii
Blakea herrerae
Blakea scarlatina
Calicina arida
Calicina basalta
Calicina conifera
Calicina diminua
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Calicina galena
Calicina mesaensis
Chiloglanis harbinger
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Holographis leticiana
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Miconia calocoma
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Miconia ligulata
Miconia peltata
Neostethus robertsi
Pachycara crossacanthum
Pachycara gymninium
Pachycara lepinium
Pachycara mesoporum
Pachycara pammelas
Pachycara rimae
Pachycara shcherbachevi
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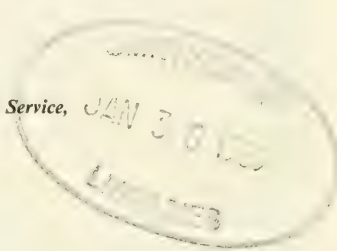
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AN ECOGEOGRAPHIC ANALYSIS OF THE HERPETOFAUNA OF
THE SIERRA SAN PEDRO MÁRTIR REGION, BAJA CALIFORNIA,
WITH A CONTRIBUTION TO THE BIOGEOGRAPHY OF THE
BAJA CALIFORNIA HERPETOFAUNA

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ABSTRACT: An ecogeographic analysis of the distributions of the herpetofauna of the Sierra San Pedro Mártir Region of Baja California was undertaken. The Mártir Region is part of northern Baja California from approximately latitude 30°N to 31°N. Over 3,000 locality records from the literature, museums, and field work were analyzed across a matrix of ecogeographic formations based on regional climates, physiography, and extant vegetation. Numerical and heuristic methods of biogeographic analysis indicated the 65 species present occur in seven distinct patterns. Examination of these contemporary patterns within and beyond the Mártir Region led to a hypothesis of five historical patterns of evolutionary development among the Baja California herpetofauna. This hypothesis indicates that vicariance, dispersal (diffusion), and in situ evolution are interacting phenomena contributing to contemporary herpetofaunal distributions in peninsular and insular Baja California and the Pacific Southwest.

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INTRODUCTION

There is a growing consensus that ecological factors limit the geographic range of all organisms (e.g., Udvardy 1969; MacArthur 1972). Rotramel (1973:229) expressed it thusly: "... biogeographic areas originate from and are maintained by the interactions of organisms with physical and biotic factors in their environments." He noted a lack of placing proper emphasis on ecological factors in biogeographic analysis, which he attributed to historical influ-

ences, and concluded that "... continued progress in solving the questions of the origins of biogeographic areas will require biogeographers to clearly distinguish the origins of species from the origins of areas and then develop new methods of eco-geographic analysis" (Rotramel 1973: 230).

The ecogeographic characteristics of a species' distribution can be viewed as the present summation of the continuous evolutionary process of interaction and compromise that occurs between that species and its environment. A new adaptation to the environment that promotes greater survivorship of offspring within an area, or population expansion into new areas, is a new characteristic of the ecological strategy of that

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species, and a new chapter in its evolutionary development. While congruent areas for different species are theoretically impossible if the areas are defined strictly in terms of the organisms' ecological niches, groups of species—both plant and animal—do coexist and coevolve in loose congruency in biotic communities. Given that the ecological parameters of a species are indicative of the historical process through which that species has evolved, it is logical to assume that a similarity of ecogeographic constraints among populations of different species in the same area may indicate a common history for those species. This common history may not have entailed direct ecological interactions but nonetheless constitutes a coevolution, where these species' distributions are similar even when examined on a scale approaching that of microhabitat. The elucidation of such similar ecogeographic patterns is the fundamental methodology of historical biogeography, and their elucidation and interpretation comprises the essence of the discipline.

The remote, mostly inhospitable, and sparsely populated peninsula of Baja California, preserved in a relatively pristine state, is an ideal natural laboratory for the study of phenomena that influence and regulate the distributions of terrestrial vertebrates. The biotic diversity and general community structure of the flora and fauna of the Baja California peninsula was reported by Nelson (1921). Schmidt (1922) made the first comprehensive study of the diverse herpetofauna of the Peninsular Region (peninsula and related islands), describing peninsular distributions on the basis of Nelson's Faunal Districts. Savage (1960) presented a classic historical analysis of the distributions of the peninsular herpetofauna, adding significantly to our understanding of the origins of these distributions and those of the entire North American herpetofauna. However, Savage's analysis had three shortcomings: (1) he assumed that the peninsula had existed as a more or less stable physiographic unit since the Eocene; (2) he chose not to incorporate vital evidence provided by the regional insular distributions; and (3) despite noting 13 different distribution patterns among the peninsular herpetofauna, he based his numerical comparison and subsequent distributional analysis on only four Herpetofaunal Areas, apparently modeled after Nelson's Faunal Districts. This resulted in an oversimplification of distri-

bution patterns and relationships, obscuring some and entirely concealing others. Nelson's (1921) Faunal Districts and Savage's slightly more refined Herpetofaunal Areas give a general picture of major herpetofaunal distribution trends on peninsular Baja California, but under close scrutiny, they fail to delineate ecological or geographic distribution barriers for much of the herpetofauna.

Greater ecological and geographical resolution is now possible with the extensive taxonomic and distributional data available from more recent studies of the regional herpetofauna. Loomis et al. (1974) compiled an updated checklist and reported the general distributions of the Baja California herpetofauna. Linsdale (1932), Tevis (1944), Murray (1955), Bostic (1971), Murphy (1975, 1976, 1983a), Welsh (1976a), Seib (1980), and Welsh and Bury (1984) have investigated community distributions in various parts of the peninsula. Numerous other authors have contributed to knowledge of distributions and ecology for single species of the regional herpetofauna (see species accounts below). However, a comprehensive ecogeographic study of the entire Baja California herpetofauna has yet to be conducted. Murphy's (1983a) study is the best attempt to date; using new distributional data from remote areas of southern Baja California and the Gulf islands, he defined more accurate southern peninsular biotic subdivisions for analysis.

Murphy lacked complete and accurate distributional data for some species in the northern areas; his analysis emphasized the southern peninsular patterns. He lumped several northern distribution patterns together in a "marginal track" and, I submit, underplayed their overall significance as evidence of important evolutionary trends complementing the tectonic events that shaped the distributions of much of the Baja California herpetofauna. The northern peninsular patterns are important because the north is the proposed "gate" for species migrating down from the continent (Savage 1960), and the majority of the lineages present in Baja California are represented there. Its diversity of habitat types, stemming from its marked elevational gradient, and from its situation between tropical and temperate latitudes, is the greatest on the peninsula.

This study focuses on the northern area of the peninsula, specifically on the Sierra San Pedro Mártir Region of north central Baja California

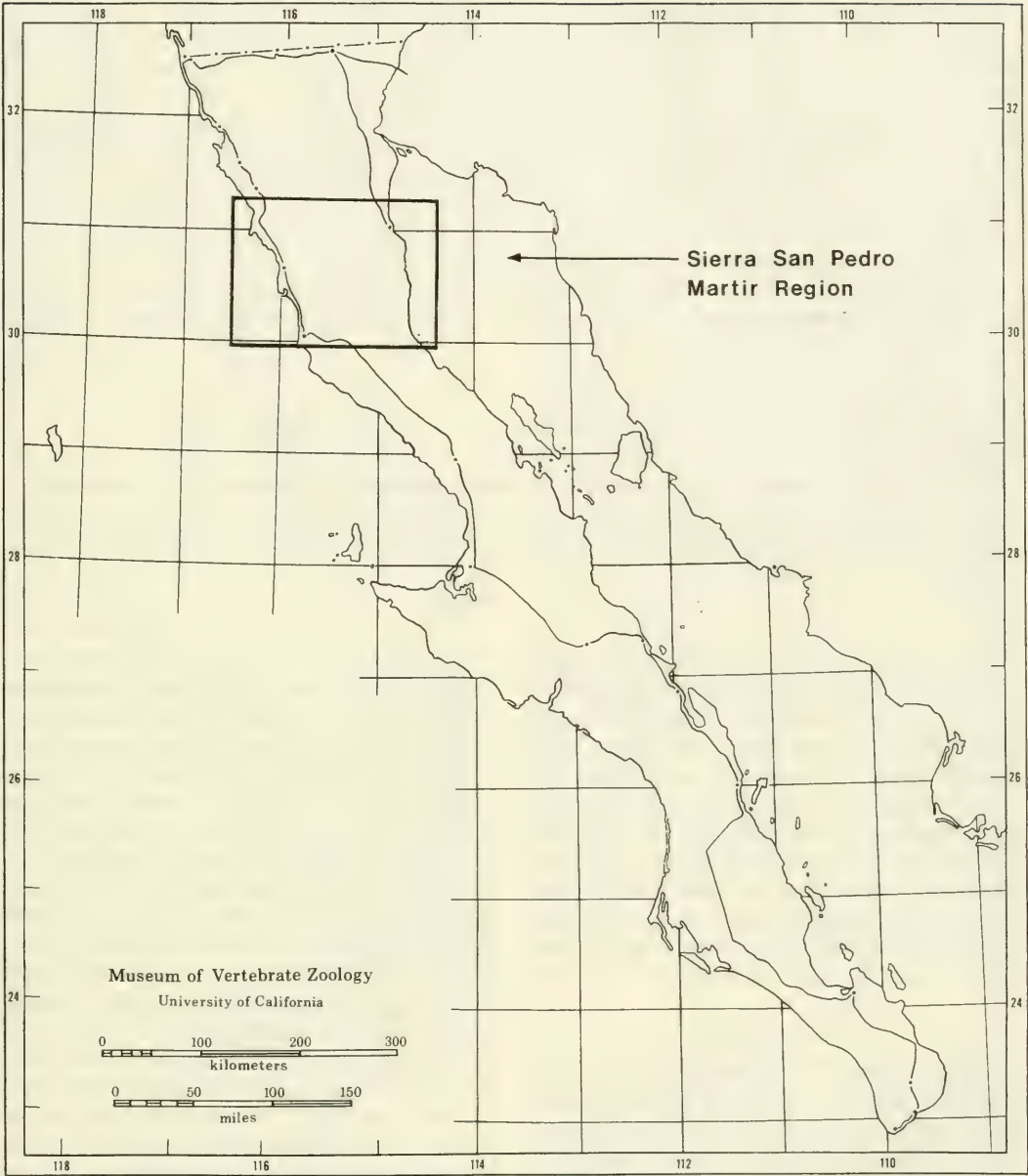


FIGURE 1. The location of the Sierra San Pedro Mártir Region, Baja California Norte, México.

(hereafter referred to as the Mártir Region, or simply the Region). The Mártir Region consists of that area of northern Baja California from approximately 30°N to 31°N latitude (Fig. 1). It contains 65 species of reptiles and amphibians. Four of Nelson's five Faunal Districts and three of Savage's four Herpetofaunal Areas intersect

within the Region (Fig. 2a). Hastings and Turner (1965) investigated the climates of Baja California. They correlated their data with the work of Shreve and Wiggins (1964) on plant distributions and described six phytogeographic divisions in Baja California. Three of these vegetation areas intersect in the Mártir Region (Fig. 2b).

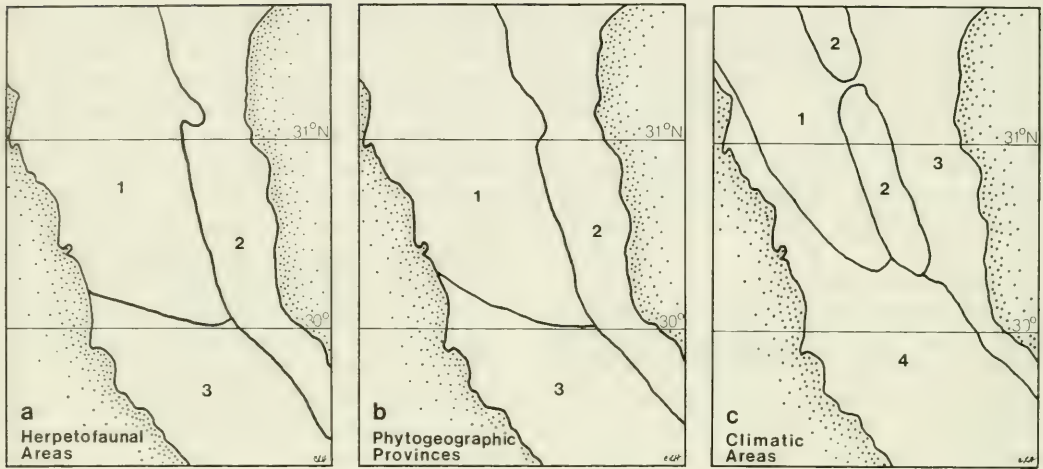


FIGURE 2. Biotic and climatic subdivisions of the Sierra San Pedro Mártir Region, Baja California, México. a) Herpetofaunal Areas (Savage 1960): (1) Californian; (2) Colorado Desert; (3) Peninsular Desert. (b) Phylogeographic Provinces (after Shreve and Wiggins [1964] and Hastings and Turner [1965]): (1) San Pedro Mártir; (2) Lower Colorado Valley; (3) Vizcaino. (c) Geographic relationships of the major climatic areas: (1) Pacific Climate; (2) Montane Climate; (3) Gulf Climate; (4) Central Desert Climate.

My approach was to formulate a base map of regional habitats with which to compare distributions and seek evidence of patterns across species. Such evidence was then used to define potential historical groupings. Independent evidence of congruency among overall distributions was then sought as corroboration for the groupings derived from the regional analysis. Such corroboration I considered as evidence that the regional groupings are each the result of a common evolutionary history among its members, and not the result of random processes.

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MATERIALS AND METHODS

The following procedures were followed in the investigations of the distributional patterns of the herpetofauna of Baja California: (1) derivation of a base map of the ecogeographic formations of the Sierra San Pedro Mártir Region on the basis of climatic data, physiographic features, and extant vegetation associations; (2)

compilation of locality and ecological data for the 65 herpetofaunal species occurring within the Mártir Region from field investigations, museum records, and available literature; (3) plotting of ecogeographic distributions of regional species, and grouping of species whose distributions are similar and thus indicative of a possible historical relationship; (4) assessment of the validity of such proposed historical groupings by comparison of intra-Regional patterns with broader distribution patterns (in the rest of Baja California and beyond), to seek corroborative evidence of a common evolutionary history.

Derivation of Regional Ecogeographic Formations

Heyer (1967:259) described a life zone as "an ecological altitudinal or latitudinal zone, characterized by specific climate parameters and secondarily by vegetation." Miller's (1951) "ecologic formations" reflected geomorphological components that sometimes play a greater role in the distribution of species than do altitudinal or vegetative parameters. I have incorporated both these concepts in my division of the Region into "ecogeographic formations." These formations were delineated on the basis of both field data and literature pertaining to physiographic features, climate, and dominant vegetational associations (using perennial plant species). Biogeographic assemblages generally represent gradients with regard to space, time, and biotic form, and boundaries between assemblages are therefore at best approximate and variable, changing continuously, and varying somewhat for each biotic form (Udvardy 1969). Therefore, I have used ecotones to establish approximate boundaries between ecogeographic formations.

Compilation of Species Accounts

The herpetofauna throughout the Mártir Region was surveyed from 22 June to 13 August 1973, from 9 April to 25 June 1974 (except 6 days in late May 1974), for 2 weeks in June 1976, and 2 weeks in May 1979. Much of the Region is accessible by road and many areas were reached by vehicle. In the more remote and inaccessible central and south central parts of the Region travel was by foot. A total of 2,187 km by road and 766 km by trail were logged during these investigations. Approximately 80–90% of the areal ex-

tent of the Mártir Region was observed. Elevation (with a barometric altimeter), physiography, climate, vegetation, and microenvironmental conditions were recorded wherever animals were observed or collected. Distributional, ecological, and behavioral data were recorded on the 65 species that comprise the herpetofauna of the Mártir Region. Two hundred thirty-one voucher specimens were collected; now deposited in the Museum of Vertebrate Zoology, University of California, Berkeley. Additional locality records of captured and released or observed animals totaled 523. Museum and literature records used in the study totaled 2,618. A total of 3,372 locality records were obtained from 65 collecting sites. The collecting sites are listed, north to south, in Appendix A, and are shown in Figure 3. Distributional data from the following museums were used: California Academy of Sciences (CAS and SU), San Diego Natural History Museum (SDNHM), Los Angeles County Museum of Natural History (LACM), and the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ). Sources for literature records are noted in the species accounts. All known localities of museum and literature records were visited to determine existing vegetational and physiographic features, and to note available habitat types. Phylogenetic organization of families in the species accounts follows Stebbins (1985). Subspecific nomenclature was used in all cases where subspecies have been described; otherwise the currently recognized species names were used. Common names used are from Collins et al. (1978) or Stebbins (1985).

Derivation of Regional Distribution Patterns

Two different methods were used to compare the distributions of regional species. Following Savage (1960) and Murphy (1983a), numerical techniques of analysis were used. Peters (1971) pointed out that although numerical methods in biogeography are capable of making quantitative distinction between areas, they cannot distinguish whether said areas have a real basis in nature. This problem was addressed by using regional ecogeographic formations as the primary areas for numerical comparison instead of pre-established faunal or vegetation provinces or the equal quadrants technique often used with numerical faunal analyses.

Secondly, a two-phased heuristic method was

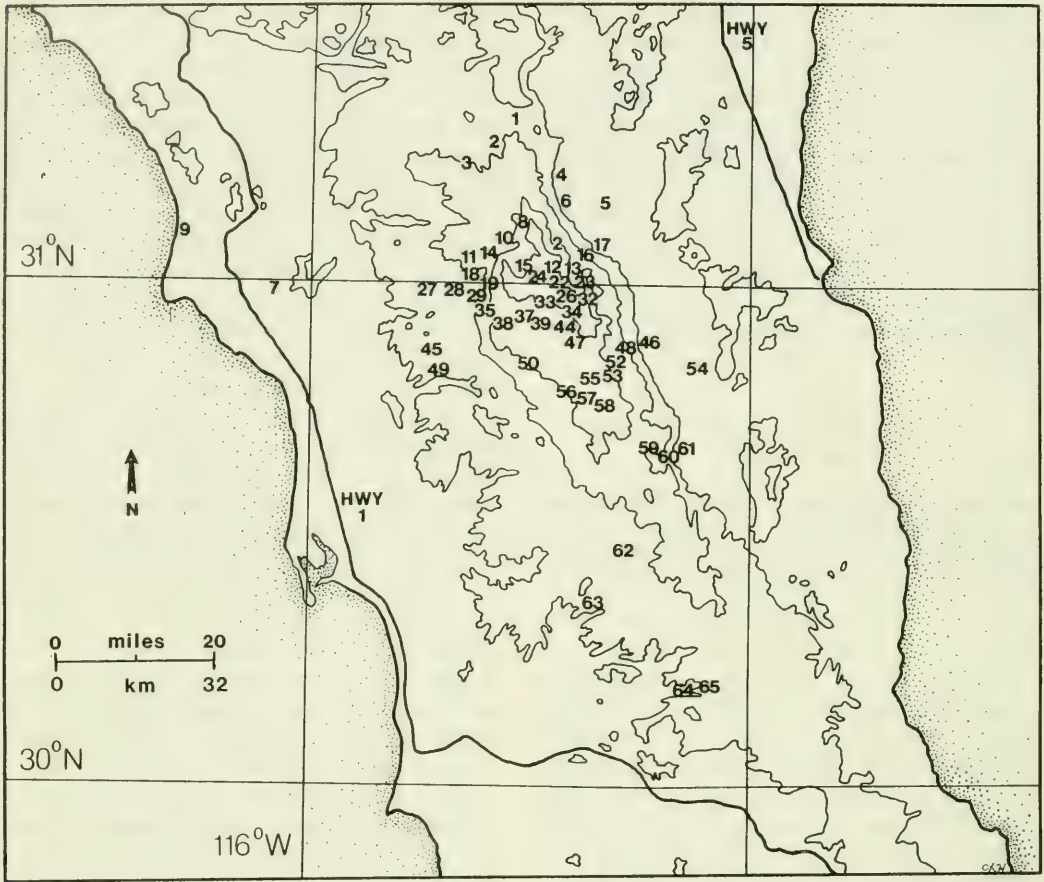


FIGURE 3. Location of collecting stations in the Sierra San Pedro Mártir Region, Baja California Norte, México. Stations 20, 21, 25, 30, 31, 36, 40–43, 51, and 60 have been omitted; these stations are adjacent to the next highest number, e.g., station 20 and 21 are near station 22. Exact locations and elevations of stations are in Appendix A. Topographic intervals equal 610 m (2,000 ft).

used to analyze regional distributions. Phase one consisted of a comparison of distributions across a transect of regional ecogeographic formations, and phase two was a comparison of overall regional distributions as plotted on maps based on Figures 3, 4, and 5.

My numerical–heuristic strategy of analysis was similar to the approach of Morafka (1977) except that he used two numerical techniques, faunal resemblance coefficients (two formulas) and an equal quadrants analysis. I used three faunal resemblance coefficients and no equal quadrants analysis. Both the numerical and heuristic methods are discussed in more detail in the section on zoogeographic analysis.

Distributions Beyond the Mártir Region

Distributional congruency beyond the Mártir Region for those taxa linked ecogeographically within the Mártir Region was considered to be indicative of possible historical links and a shared evolutionary history. Evidence for such extra-regional congruency was sought using independent means. The method of establishing and comparing the combined distributions of related forms, conspecific or congeneric, or both (individual tracks), in order to establish or deny broad geographical congruency between unrelated taxa—and thus demonstrate more general distribution patterns (generalized tracks)—follows

the principles and method indicated by Croizat (1964).

RESULTS

THE ENVIRONMENT

The Sierra San Pedro Mártir Region refers to that area of northern Baja California between the Pacific Ocean, the Gulf of California (Sea of Cortez), and latitudes $31^{\circ}20'N$ and $30^{\circ}00'N$ (Fig. 1), an area of approximately 150 km^2 . The mountain range central to the Region, the Sierra San Pedro Mártir, hereafter referred to as the Sierra, is over $3,000 \text{ m}$ in elevation, and transects the center of the Mártir Region from north to south. The Colorado Desert is east of the Sierra, and foothill ranges and the San Quintín Plain are to the west. The Mártir Region is at the southern extreme of the north temperate zone and is influenced by two diverse climates, the Pacific and Gulf regimes (Hastings and Turner 1965).

Physiographic Features

The topography and geography of the Sierra San Pedro Mártir were described by Nelson (1921) and Henderson (1960). Woodford and Harris (1938) described the geology and geomorphology of the Region, and Allison (1964) discussed the topographic relationships of the Mártir Region with the features of surrounding regions.

Information on the general physiography of the Mártir Region was obtained from topographic maps (Estados Unidos Mexicanos, Series 501), flight navigation charts (U.S. Dept. Commerce CH-22, 1979), and Robinson (1972). Based on these sources and my field investigations, I subdivided the Region into nine primary topographic elements, each with a unique and relatively homogeneous physiography (Fig. 4).

The Sierra consists of an elevated, granitic fault block dated from the mid-Cretaceous (Silver et al. 1956). The fault block is a segment of the Baja California Cordillera, and is considered part of the Peninsular Range Physiographic Province (Allison 1964), which extends from the Transverse Ranges of southern California (at the latitude of Los Angeles) south along the length of Baja California.

The northern extremity of the Sierra is at San Matías Pass (980 m), which is probably a trans-

verse fault (Allen et al. 1956). The southern extremity of the Sierra is in the vicinity of Cerro Matomí ($30^{\circ}24'N$, $115^{\circ}10'W$), south of which the Sierra gradually decreases in elevation and is covered by lava-capped mesas. Here, the mountains grade into the North Central Desert. The area from Cerro Matomí south to $30^{\circ}N$ latitude was designated the North Central Desert Topographic Element (Fig. 4).

The eastern slope of the Sierra, designated the East Scarp Topographic Element (Fig. 4), is a steep and fairly straight fault scarp rising $1,220$ – $2,120 \text{ m}$ above the desert floor. A series of steep canyons transect this scarp, and terminate in piedmont alluvial fans, opening onto Valle de San Felipe and Valle Chico, two continuous desert valleys paralleling the scarp base at about 600 m elevation. These valleys are part of, and contiguous with, the southern Colorado Desert. The Colorado Desert extends from California and Arizona, south along the Gulf coast of Baja California to the vicinity of Bahía de Los Angeles ($29^{\circ}00'N$, $113^{\circ}15'W$). This desert from $31^{\circ}20'N$ latitude south to Bahía de Los Angeles was designated the South Colorado Desert Topographic Element (Fig. 4). All topographic elements from the ridge of the East Scarp, east to the Gulf of California, comprise the Gulf Slope.

The west slope of the Sierra consists of a series of lesser fault scarps with intervening steps between that drop more gradually than the East Scarp. They range from 915 m to $1,525 \text{ m}$. This area is designated the West Scarp Topographic Element. Below the West Scarp Topographic Element is a series of foothill ranges that drop gradually to a coastal plain. The foothill ranges and the coastal plain are designated the Western Foothills, and the San Quintín Plain Topographic Elements, respectively (Fig. 4).

The corrugated Main Scarp of the Sierra San Pedro Mártir is 13 – 16 km wide, 64 km long, and is bordered and transected by irregular, boulder-stacked ridges. The Main Scarp contains four major, and numerous minor, alluvial-filled, meadow expanses; several of these meadows contain year-round surface water. The Main Scarp was subdivided into the Upper Main Scarp Topographic Element, consisting of those areas north of Tasajera Ridge and above $2,300 \text{ m}$ ($7,550 \text{ ft}$), and the Lower Main Scarp Topographic Element, consisting of those areas south of Tasajera Ridge and below $2,300 \text{ m}$ (Fig. 4). Tasajera Ridge

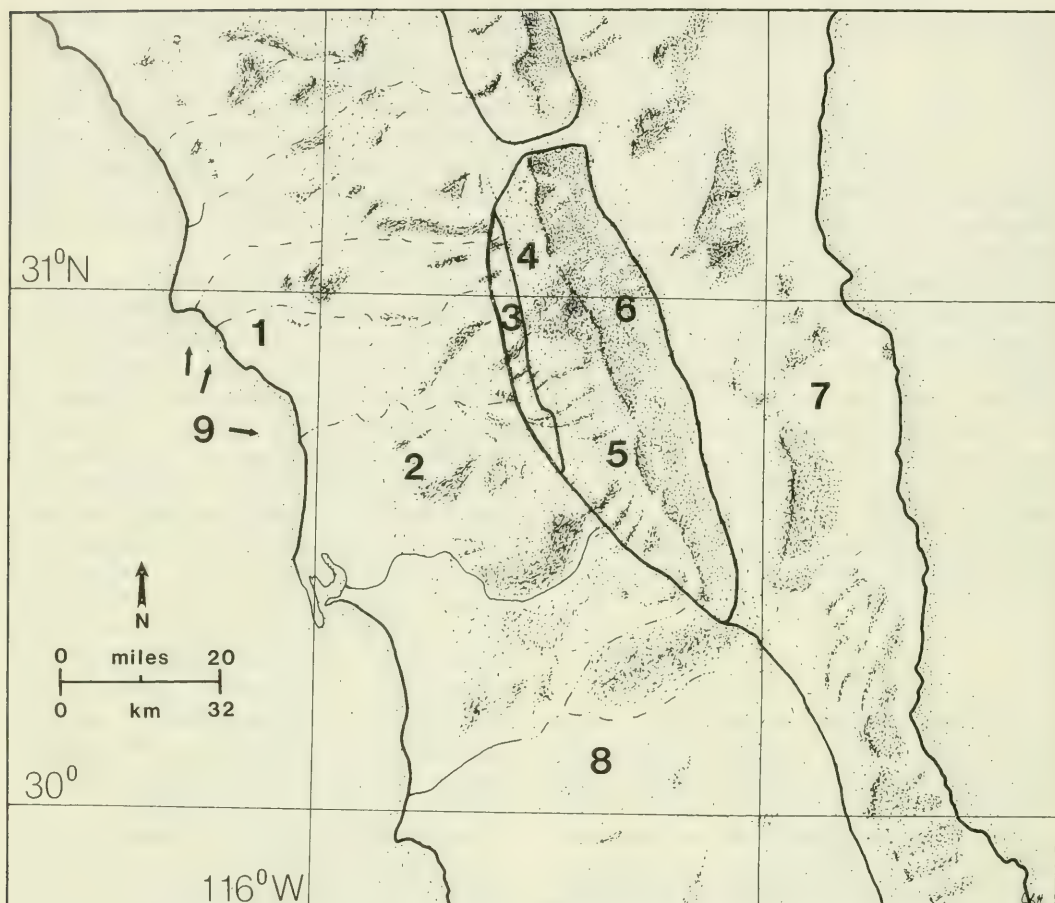


FIGURE 4. Geographic relationships of the major topographic elements of the Sierra San Pedro Mártir Region, Baja California Norte, México. (1) San Quintín Plain; (2) Western Foothills; (3) West Scarp; (4) Upper Main Scarp; (5) Lower Main Scarp; (6) East Scarp; (7) South Colorado Desert; (8) North Central Desert; (9) Western Arroyos.

transects the Main Scarp at about midlength, and runs west to east at $30^{\circ}57'N$ latitude.

The Pacific Slope is west of the crest of the Sierra San Pedro Mártir and north of the North Central Desert Topographic Element (Fig. 4). It is transected by a system of westerly directed canyons, carrying partly subterranean runoff from the Sierra, 72 km west to the Pacific. These arroyos were designated the Western Arroyos Topographic Element (Fig. 4). In subsequent sections, the suffix "Topographic Element" has been omitted, and the capitalized geographic entity is used to designate these topographic divisions (e.g., West Scarp Topographic Element = West Scarp).

Regional Climates

The climate of the Mártir Region results from the interaction of regional topography with two major climatic regimes that govern weather conditions over most of Baja California. The climatic regimes consist of the relatively cool, moist Pacific Coastal Regime, produced by the cold California Current with its prevailing westerly winds, and the considerably warmer drier Gulf Regime (Hastings and Turner 1965; Meigs 1966).

Hastings and Turner (1965) postulated that seasonal differences in variability and amount of precipitation produce the distinctive vegetation-

al associations of their phytogeographic provinces (Fig. 2b). Lacking quantitative data, they lumped the Sierra San Pedro Mártir with all of northwestern Baja California in the San Pedro Mártir Phytogeographic Province. My observations within this province indicated more complex vegetational relationships. I found this montane area to have a climate and vegetation sufficiently unique to warrant separate consideration.

The Sierra has predictable winter and spring precipitation, often falling as snow in the winter (J. Alonso, Mexican National Observatory, pers. comm.). A summer rainfall pattern results from a thermal low pressure cell to the east of the Sierra, causing moist air to flow east across the mountains. Afternoon thunder showers occur almost daily from late June through September as a result of orographic uplift. Data from San Juan de Dios (elevation 1,400 m) in the Sierra Juárez, 144 km north of the Sierra San Pedro Mártir, show the highest annual precipitation (33.4 cm) yet reported for northern Baja California (Hastings and Humphrey 1969). The Main Scarp of the Sierra San Pedro Mártir is considerably higher in elevation than the Sierra Juárez and thus probably receives the highest annual precipitation in Baja California.

The precipitation percolates down through the granitic sand and the soil surface dries rapidly in the warm summer air. Flash-flooding from unusually heavy rainfall occurs occasionally on all scarps. Lightning regularly accompanies these storms and is responsible for fires on the forested plateau. Underbrush is scarce throughout much of the forest, perhaps due to fires.

The Main Scarp, and the upper reaches of the West and East scarps, areas influenced by the high elevation weather system of the Sierra, have been designated the Montane Climatic Area (Fig. 2c).

Those areas on the west side of the Sierra San Pedro Mártir, encompassing the lower elevations of the West Scarp, the Western Foothills, and the Western Arroyos were designated the Pacific Climatic Area (Fig. 2c). This area is characterized by frequent fog, cool oceanic temperatures, and relatively predictable winter and spring precipitation (Table 1, Western Foothills).

Those areas on the east slope of the Sierra San Pedro Mártir, and corresponding with the southern portion of the Lower Colorado Valley Phy-

togeographic Province (Table 1), were designated the Gulf Climatic Area; it encompasses the lower East Scarp and the South Colorado Desert Topographic Elements (Fig. 2c; Table 1). This area is one of the hottest places in the world (Meigs 1953) and is characterized by a lack of predictable rainfall. Shreve (1934) remarked that this area may be the most sparsely vegetated of any in North America.

The area designated the Central Desert Climatic Area corresponds with the northern portion of the Vizcaino Phytogeographic Province (Table 1), and encompasses the North Central Desert Topographic Element (Fig. 2c; Table 1). This area has the driest summers of the four climatic areas. The lack of rainfall in the Central Desert is mitigated by cool Pacific air and frequent fogs, which provide considerable ground moisture. Bostic (1971) described the climate of the Central Desert in greater detail.

The narrow San Quintín Plain Topographic Element, extending northward to the vicinity of latitude 30°20'N, was included in the Central Desert Climatic Area (Fig. 2c). Hastings and Turner (1965) included this area with northwestern Baja California, placing it in their San Pedro Mártir Phytogeographic Province. Climatic data from this coastal plain were analyzed and compared with similar data from adjacent topographic elements to the northeast and south (Table 1). The climate of the San Quintín Plain falls between that of the two adjacent areas, but seasonal precipitation patterns are most similar to the Central Desert Climatic Area. Floral and faunal characteristics of the San Quintín Plain indicate that this area, and the proximate inland valleys, are within the influence of the Central Desert Climate (Short and Crossin 1967; Bostic 1968; this study).

References to the four climatic areas of the Mártir Region will use this format: Gulf Climatic Area = Gulf Climate.

Vegetative Elements

Following the approach of a similar regional study conducted by Schoenherr (1976) in the San Gabriel Mountains of southern California, the structure and distribution of Mártir Region vegetation communities were determined. Nelson (1921) reported on an extensive natural history survey of Baja California, and described vege-

TABLE 1. SUMMARY OF CLIMATIC DATA FROM THE SIERRA SAN PEDRO MÁRTIR REGION, BAJA CALIFORNIA NORTE, MÉXICO; REPORTED BY PHYTOGEOGRAPHIC PROVINCE AND TOPOGRAPHIC ELEMENT (FIG. 4).

Geographic area	Winter	Spring	Summer	Fall	Annual	Number of weather stations ¹
Mean precipitation (cm)						
Phytogeographic province ²						
Lower Colorado Valley	1.9	0.8	1.4	2.0	6.1	8
Vizcaíno	5.6	1.0	1.1	2.8	10.5	13+
San Pedro Mártir	9.2	4.1	1.8	2.7	17.8	27
Topographic element ³						
South Colorado Desert	2.3	0.7	1.3	2.0	6.5	2
San Quintín Plain	8.1	2.8	1.6	2.1	13.5	4
North Central Desert	5.5	1.3	0.4	2.1	9.5	3
Western Foothills	9.7	3.5	4.0	4.3	18.9	7
Sierra Scarps ⁴					(33.4)	0
Mean temperature (°C)						
Topographic element						
South Colorado Desert	15.0	21.8	31.8	24.8	23.2	2
San Quintín Plain	13.2	15.2	19.3	18.0	16.4	4
North Central Desert	13.4	16.3	23.3	19.5	19.1	3
Western Foothills	11.9	16.6	22.7	18.7	17.2	7
Sierra Scarps			(no data)			0

¹ See Hastings and Humphrey (1969) for exact locations.
² Data from Hastings and Turner (1965).
³ Mean precipitation and temperature data were summarized from weather stations within each topographic element; data are from Hastings and Humphrey (1969).
⁴ Data from Sierra Juárez; see text.

tational characteristics and listed dominant species in accordance with Merriam's (1898) life zones. Wiggins (1944) surveyed the Sierra San Pedro Mártir and surrounding lowlands, Shreve (1936) described the complex vegetation west of the Sierra, and Chambers (1955) described the flora of a canyon on the East Scarp.

Seven vegetational associations are recognized within the Mártir Region (Fig. 5): Coniferous Forest, Chaparral, Pinyon-Juniper Woodland, Creosote Bush Scrub, Coastal Sage Scrub, Central Desert Scrub, and Riparian Woodland. These vegetational associations are modeled after the communities of Munz and Keck (1949, 1959) except where noted below. The dominant species of each association are listed in Table 2.

Coniferous Forest

Coniferous Forest vegetation occurs above 1,830 m on the Sierra Main Scarp, within areas influenced by the Montane Climate (Fig. 5, 6). The forest is open and parklike, with sparse undergrowth of low shrubs, forbs, and grasses.

At higher elevations (over 2,400 m), vegeta-

tional elements characteristic of Merriam's (1898) Canadian and Hudsonian zones (lodgepole pine [*Pinus murrayana*], white fir [*Abies concolor*], and quaking aspen [*Populus tremuloides*]) are intermixed with the dominant elements of Coniferous Forest. This impoverished boreal vegetation is best developed in deep canyons and on north-facing slopes of the Upper Main Scarp at the north end of the Sierra.

Chaparral

Chaparral covers extensive areas of the Pacific Slope of the Sierra, between 1,220 m and 2,120 m, and occurs in a narrow belt on the East Scarp between 1,670 m and 2,120 m (Fig. 5, 7). The dense and often impenetrable vegetation is commonly 2.5–3.0 m in height. Distribution of Chaparral on both versants corresponds with the steep scarp faces where the Montane Climate intergrades with the drier and warmer Pacific and Gulf climates.

Within the Chaparral, and particularly in shaded canyons and areas with surface and sub-surface water, are patches of oak woodland. Oak

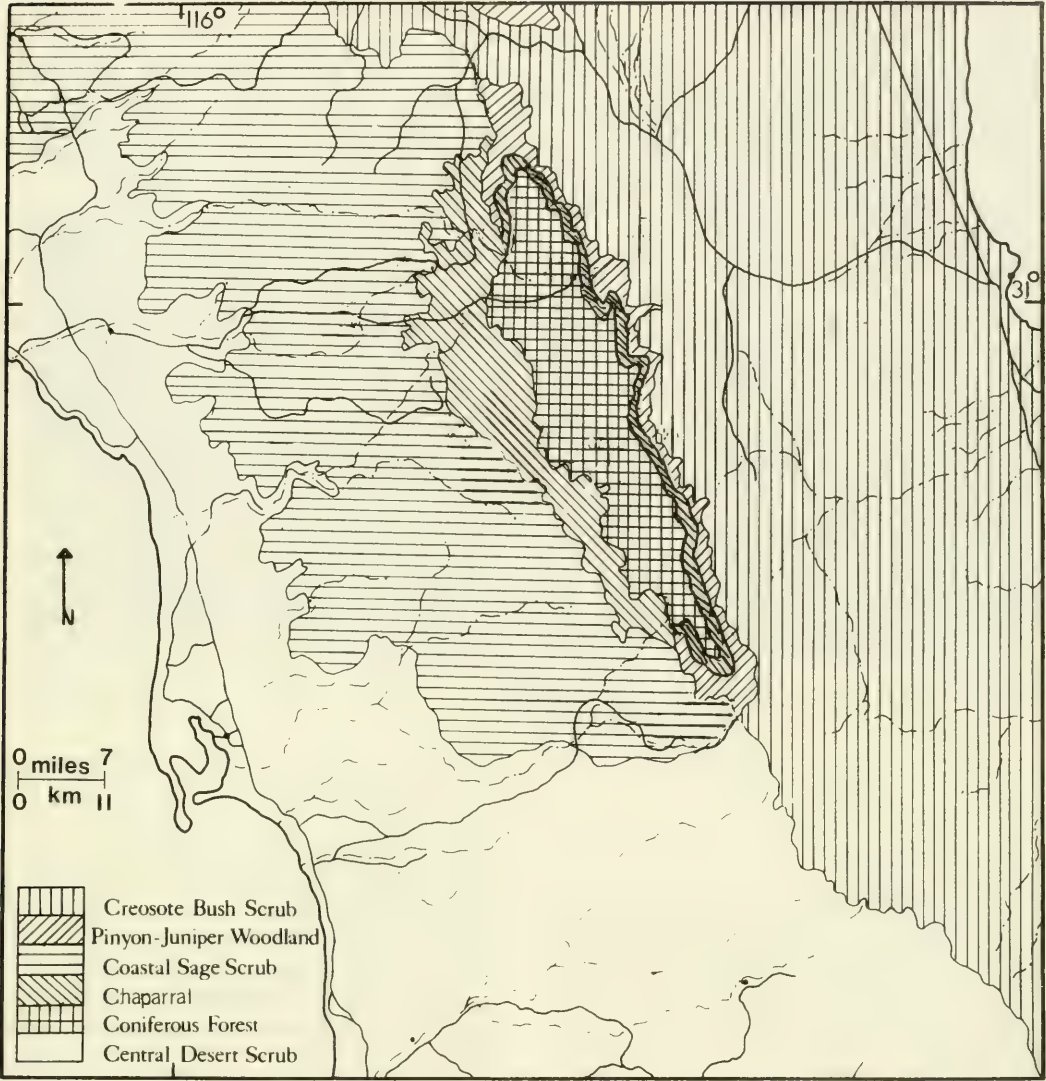


FIGURE 5. Vegetational associations of the Sierra San Pedro Mártir Region, Baja California Norte, México. Map is based on U.S. Dept. Commerce, CH-22 (1979). Distribution of vegetation is based on Shreve and Wiggins (1964), Short and Crossin (1967), and field investigations. Riparian Woodland Association occurs in all other vegetation types.

woodland in the Sierra San Pedro Mártir occurs primarily as riparian habitat, and is considered with the Riparian Woodland association.

Pinyon-Juniper Woodland

This vegetational type occurs between 920 m and 1,830 m on the East Scarp of the Sierra (Fig. 5, 8); this distribution coincides with areas of higher elevation dominated by the Gulf Climate.

Being high on the east versant of the Sierra, Pinyon-Juniper Woodland is probably also influenced to some degree by the Montane Climate. The trees in the Pinyon-Juniper Woodland vary from approximately 3.0 to 10.0 m in height, and are widely dispersed. Open shrub growth occurs throughout the Woodland. This association extends around the southern and northern ends of the range above 920 m and intergrades with Chaparral.

TABLE 2. DOMINANT SPECIES OF THE VEGETATIONAL ASSOCIATIONS OF THE SIERRA SAN PEDRO MÁRTIR REGION, BAJA CALIFORNIA NORTE, MÉXICO.

Vegetation association	Dominant species
Coniferous Forest	jeffery pine (<i>Pinus jeffreyi</i>), sugar pine (<i>P. lambertiana</i>), incense-cedar (<i>Libocedrus decurrens</i>), rose sage (<i>Salvia pachyphylla</i>), greenleaf manzanita (<i>Arctostaphylos patula</i>), pink-bracted manzanita (<i>A. pringlei</i>), snow bush (<i>Ceanothus cordulatus</i>), scrub oak (<i>Quercus</i> spp.)
Coastal Sage Scrub	flattop buckwheat (<i>Eriogonum fasciculatum</i>), California sagebrush (<i>Artemisia californica</i>), white sage (<i>Savia apiana</i>), century plant (<i>Agave shawii</i>), prickly pear (<i>Opuntia littoralis</i>), coastal cholla (<i>Opuntia prolifer</i> a), <i>Ephedra californica</i>
Pinyon–Juniper Woodland	pinyon pine (<i>Pinus monophylla</i> and <i>P. quadrifolia</i>), California juniper (<i>Juniperus californica</i>), Mojave yucca (<i>Yucca schidigera</i>), barrel cactus (<i>Ferocactus acanthodes</i>), <i>Agave aurea</i> , scrub oak (<i>Quercus turbinella</i>), sugar bush (<i>Rhus ovata</i>)
Central Desert Scrub	datilillo (<i>Yucca valida</i>), elephant tree (<i>Pachycormus discolor</i>), century plant (<i>Agave shawii</i>), cardon (<i>Pachycereus pringlei</i>), cholla (<i>Opuntia</i> spp.), <i>Franseria chenopodiafolia</i> , Ocotillo (<i>Fourquiera splendens</i>), <i>Dudleya</i> spp.
Chaparral	bigberry manzanita (<i>Arctostaphylos glauca</i>), Mexican manzanita (<i>A. pungens</i>), chamise (<i>Adenostoma fasciculatum</i>), ceanothus (<i>Ceanothus leucodermis</i> and <i>C. greggi</i>), toyon (<i>Heteromeles arbutifolia</i>), red shank (<i>Adenostoma sparfolium</i>), scrub oak (<i>Quercus dumosa</i>), sugar bush (<i>Rhus ovata</i>)
Creosote Bush Scrub	creosote bush (<i>Larrea tridentata</i>), white bursage (<i>Franseria dumosa</i>), ocotillo (<i>Fourquiera splendens</i>), mesquite (<i>Prosopis juliflora</i>), agave (<i>Agave</i> spp.), palo verde (<i>Cercidium microphyllum</i>), yucca (<i>Yucca</i> spp.), ironwood (<i>Olneya tesota</i>), cholla (<i>Opuntia</i> spp.), catclaw (<i>Acacia greggi</i>), cardon (<i>Pachycereus pringlei</i>)
Riparian Woodland (Species composition varies greatly with elevation and slope; abbreviations refer to correspondence with above associations.)	willow (<i>Salix</i> spp.), wild rose (<i>Rosa californica</i>), jeffery pine (<i>Pinus jeffreyi</i>), incense-cedar (<i>Libocedrus decurrens</i>) (CF); Oak (<i>Quercus</i> spp.), coffeeberry (<i>Rhamnus californica</i>) (Chp); Cottonwood (<i>Populus fremonti</i>) (P-J, CSS); Sycamore (<i>Platanus racemosa</i>), ceanothus (<i>C. leucodermis</i> and <i>C. greggi</i>) (CSS); mesquite (<i>Prosopis juliflora</i>), desert willow (<i>Chilopsis linearis</i>) (CBS and CDS); fan palm (<i>Washingtonia filifera</i>) (CDS)

Creosote Bush Scrub

Creosote Bush Scrub occurs below 1,070 m on the eastern side of the Sierra, in the influence of the Gulf Climate (Fig. 5, 9). The physiognomy of this vegetation is predominantly shrub, 0.7–4.8 m tall, and widely dispersed. Creosote Bush Scrub vegetation becomes more luxuriant along the base of the East Scarp, and to a lesser degree along the immediate Gulf coast of the South Colorado Desert. Qualitative observations suggest more plant species occur in these two marginal parts of the South Colorado Desert and the shrubs and cacti attain greater size here than in much of the central area of the desert. This phenomenon may be a result of increased surface or sub-surface moisture, as Gulf Slope runoff (from the East Scarp and South Colorado Desert), which is primarily subterranean, is nearest the surface in these areas.

Fieldwork in the South Colorado Desert was restricted primarily to the basal slopes of the Sierra, and the two proximate desert valleys, Valle de San Felipe and Valle Chico. The Creosote

Bush Scrub classification is expanded to include the entire South Colorado Desert, south to latitude 29°N, following Shreve and Wiggins (1964). At the north end of the Sierra, Creosote Bush Scrub extends over San Matías Pass (980 m) into Valle de Trinidad, where it intergrades with Coastal Sage Scrub. South of the Sierra San Pedro Mártir (beyond 30°25'N), Creosote Bush Scrub intergrades with Central Desert Scrub along the Baja California Cordillera.

Coastal Sage Scrub

The Pacific Slope below 1,220 m, from slightly beyond the north limit of the Mártir Region, south to the vicinity of latitude 30°15'N, is vegetationally complex. Shreve (1936) described this area from Arroyo Santo Tomás to Arroyo Socorro as being within a 10-mi transition zone (from north to south) between Chaparral and Sonoran Desert vegetation. However, the classification Coastal Sage Scrub was adopted as best reflecting the life-forms and species composition that dominate most of this area (Fig. 5, 10). The



FIGURE 6. The Lower Main Scarp Ecogeographic Formation at Rancho Viejo (station 37) in Coniferous Forest adjacent montane meadow.

plants are mostly "half-shrubs, one to five feet tall or somewhat woodier and larger, forming a more open community than chaparral" (Munz and Keck 1949:97). There are numerous locations along the lower Pacific Slope of the Region where elements of desert vegetation dominate. The most extensive of these areas is the San Quintín Plain (Fig. 11) and the valleys and low slopes immediately to the east. The Chaparral occurring on the lower Pacific Slope, with the exception of scattered stands at high elevations in the Western Foothills, is mostly dwarfed and depauperate. The desert scrub and Chaparral complexes are not the primary associations of the lower Pacific Slope.

Central Desert Scrub

The scrub vegetation changes noticeably in the vicinity of latitude $30^{\circ}15'N$ on the Pacific Slope. The Creosote Bush Scrub of the lower East Scarp and Colorado Desert drainages, the Coastal Sage Scrub of the Western Foothills, and the Chaparral of the southern Sierran slopes interdigitate with a Sonoran vegetation characterized by sarcophyllous forms. Wiggins (1960) described this area as part of the Central Desert Phytogeograph-

ic Area of the Vizcaíno Province. Following the work of Aschman (1959), Wiggins (1960), and Bostic (1971), I also considered this area to have a unique biota. The plant association of this area is referred to as Central Desert Scrub in order to locate it geographically and to indicate its close structural relationship to the aforementioned scrub vegetational associations (Fig. 5, 12).

This classification is applicable to the vegetation of the San Quintín Plain, to the vicinity of latitude $31^{\circ}20'N$. Central Desert Scrub vegetation is denser and more lush on the San Quintín Plain than in the North Central Desert. Sarcophyllous forms dominate in many areas here, often occurring in impenetrable stands. Bostic (1971) noted that many of these plants are adapted structurally to collect moisture from the air (*Yucca valida*, *Agave* spp., *Dudleya* spp.). The regular fog and dew along this Plain probably provide a major source of water for these plants and explain the rich vegetation here.

Riparian Woodland

This plant association (Fig. 13) is based primarily on similarities of growth form and physical setting rather than simply on associations of



FIGURE 7. The West Scarp Ecogeographic Formation in Arroyo San Rafael (station 10). The vegetation is primarily Chaparral, with elements of Pinyon-Juniper Woodland and Riparian Woodland evident on the lower slopes and in the canyon bottom, respectively. The Upper Main Scarp Ecogeographic Formation is in the background.

plant species. Each of the previously described vegetational associations contains a riparian element, with only a few species common to all riparian elements. The species vary considerably relative to elevation, however the presence of closed overstory, dense understory thickets, and lush, moist ground vegetation is common to the Riparian Woodland at all elevations of the Mártir Region. The protective cover and microclimatic conditions provided by riparian areas are important for many of the reptiles and amphibians in the Region.

The most prevalent plant species in riparian associations are willows (*Salix* spp.). They compose most of the vegetation in the dense understory thickets characteristic of the riparian corridors, and they are also a major component of the overstory. In proximity to Creosote Bush Scrub and Central Desert Scrub, willows are rare and are generally replaced by mesquite (*Prosopis juliflora*) and desert willow (*Chilopsis linearis*).

Grasses, sedges, and herbs form a dense mat of streamside meadow throughout riparian associations. This meadow is most highly developed within the Coniferous Forest, where extensive areas of wet meadow occur with little or no

overstory. In scrub associations, meadow vegetation is reduced to narrow strips at streamside, rarely more than 1 m wide.

Ecogeographic Formations

On the basis of the physiographic, climatic, and vegetational data presented above, I have divided the Mártir Region into nine component ecosystems or ecogeographic formations (Fig. 14). Boundaries of the nine topographic elements closely approximate the ecotonal boundaries of the ecogeographic formations. For practical purposes, these boundaries will subsequently be treated as synonymous and each ecogeographic formation will be identified by its topographic component (Fig. 4). For the zoogeographic analysis, specimens were recorded first by vegetational association and secondarily by geographic locale. Thus, a specimen present in Chaparral on the Lower Main Scarp was scored in ecotonal vegetation on the Lower Main Scarp Ecogeographic Formation.

From west to east and from north to south, the nine ecogeographic formations of the Sierra San Pedro Mártir Region are: San Quintín Plain



FIGURE 8. The East Scarp Ecogeographic Formation in upper Cañón El Cajón (near station 51) in Pinyon-Juniper Woodland.

Ecogeographic Formation (northwest) (Fig. 11), North Central Desert Ecogeographic Formation (southwest) (Fig. 12), Western Foothills Ecogeographic Formation (Fig. 10), Western Arroyos Ecogeographic Formation (Fig. 13), West Scarp Ecogeographic Formation (Fig. 7), Upper Main Scarp Ecogeographic Formation (north) (see Fig. 7), Lower Main Scarp Ecogeographic Formation (south) (Fig. 6), East Scarp Ecogeographic Formation (Fig. 8), and South Colorado Desert Ecogeographic Formation (Fig. 9).

SPECIES ACCOUNTS

(see Appendix A for a list of collecting stations)

CAUDATA

Plethodontidae

Batrachoseps pacificus major (Camp, 1915),
Garden Slender Salamander

Batrachoseps pacificus ssp.
San Pedro Mártir Slender Salamander

Batrachoseps pacificus major is known in northwestern Baja California south to Arroyo El Rosario (K. Yanev, pers. comm.). It is known from Colonett (LACM 34331–35) and from near Santo Tomás (MVZ 55102–12). Other localities are more common northward.



FIGURE 9. The South Colorado Desert Ecogeographic Formation near the Junction of Mexico Hwy 3 and 5 in Creosote Bush Scrub vegetation.

An undescribed subspecies of *B. pacificus* (see Yanev 1978) is known locally only from the upper scarps of the Sierra San Pedro Mártir down to 1,785 m elevation.

Brame and Murray (1968) speculated that *Batrachoseps pacificus major* and *Batrachoseps pacificus* ssp. are sympatric in the Sierra San Pedro Mártir. I found no records of *B. p. major* in the Mártir Region, east of Santo Tomás, 20 km from the Pacific coast. Apparently suitable habitat for *Batrachoseps* occurs inland along the arroyos of the Western Foothills, but surface moisture in these arroyos is seldom permanent, or dependable.

I collected a gravid female of *Batrachoseps pacificus* ssp. on 24 June 1973 at station 25 (MVZ 140701). Two individuals were observed beneath a log on moist sand in a clump of willow on 21 June 1974 at station 36. Other specimens are known from Arroyo Encantada (station 41; CAS 57219–32), Encantada Meadow (SDNHM 4132–36), and La Grulla (SU 12943). All of these localities correspond with riparian woodland habitat of the coniferous forest. *B. pacificus* ssp. also occurs in riparian habitat in the chaparral on the West Scarp. I collected two specimens

inside rotting logs in oak woodland on 11 April 1974 near station 29 at 1,785 m elevation (MVZ 140702–03); a series from La Zanja Creek (SU 12933–42) is from similar habitat.

SALIENTIA

Pelobatidae

Scaphiopus couchii Baird, 1854,
Couch's Spadefoot

Wasserman (1970) indicates that *Scaphiopus couchii* is restricted to the Colorado Desert, and southward along the Gulf Slope to the Cape Region of southern Baja California. He lists no records on the Pacific slope of Baja California north of the Magdalena Plain. A specimen collected on Hwy 1, 5.3 km south junction of Hamilton Ranch Road, Valle de San Quintín (CAS 94808) and reported by Welsh (1976a) as possibly *S. couchii*, is actually a juvenile *S. hammondii*.

Scaphiopus hammondii Baird, 1854,
Western Spadefoot

This toad is known from several localities on the Pacific Slope of Baja California north of the



FIGURE 10. The Western Foothills Ecogeographic Formation 12 km west of Rancho San José (station 27) in Coastal Sage Scrub vegetation.

Mártir Region. Within the Mártir Region, Linsdale (1932) reports it from Rancho San José (station 27) in the Western Foothills; it is known also from the northern San Quintín Plain at San Antonio del Mar (SDNHM 42095–96), 32 km south of San Vicente (LACM 90967–68), along Mexican Hwy 1, 5.3 km south junction of Hamilton Ranch Road, Valle de San Quintín (CAS 94808), and 10 km south of San Quintín (SDNHM 41404). These are areas of coastal sage and central desert scrub.

Bufonidae

Bufo boreas halophilus Baird and Girard, 1852a,
California Toad

This toad is abundant in the riparian meadows and woodlands of the coniferous forest, occurring up to 2,800 m in or near riparian areas of the entire Pacific Slope; it is uncommon in the Western Foothills and in coastal areas. It frequents areas near standing or slow-flowing water.



FIGURE 11. The San Quintín Plain Ecogeographic Formation between Mexican Hwy 1 and San Antonio Del Mar (station 9). The vegetation is Central Desert Scrub with elements of Coastal Sage Scrub.

Its southernmost locality is El Rosario (CAS 136714–15).

Adults are primarily nocturnal; diurnal surface activity in the summer was observed on the Main Scarp, but mostly during afternoon cloud cover or showers. Newly metamorphosed juveniles, common in late spring in the wet meadows of the Main Scarp, were continuously active, often in direct sun. Two incidences of cannibalism were observed among these juveniles.

Adult specimens were collected at stations 3 (MVZ 140712), 26 (MVZ 140704–05), 37 (MVZ 140706–07), and 43 (MVZ 140710); adults were observed at stations 27, 29, 44, 47, 57, 58, and

62. Juveniles were collected 29 June 1973 at station 43 (MVZ 140708–09) and 23 July 1973 at station 15 (MVZ 140711). They were observed between these dates at stations 12, 15, 27, 39, and 43. Larvae were observed or collected 25 June 1973 at station 22 (MVZ 140727) and 31 July 1973 at station 15.

Bufo microscaphus californicus (Camp, 1915),
Arroyo Toad

This toad is uncommon on the Lower Main Scarp in riparian habitats of the coniferous forest; 2,300 m was the highest recorded elevation.



FIGURE 12. The North Central Desert Ecogeographic Formation at San Juan de Dios (station 64) in Central Desert Scrub vegetation.

In riparian habitats in the chaparral of the West Scarp, they are common and also abundant in riparian habitats in coastal sage scrub at the West Scarp base. Tevis (1944) found this species at the Hamilton Ranch (Rio Santo Domingo) on the San Quintín Plain; this apparently is the southernmost record in Baja California.

In the San Bernardino Mountains of California where *B. microscaphus* is sympatric with *B. boreas*, the latter species occurs in cooler, moister habitats (Cunningham 1962). My observations of the microhabitat affinities of *B. boreas* and *B. microscaphus* in the Mártir Region concur with

those reported by Cunningham. Additionally, I found *B. microscaphus* only in or near fast-flowing water, whereas *B. boreas* occurred only in or near standing or slow-flowing water. It is apparently not known whether these two species of *Bufo* deposit their eggs in different habitats or their larvae show different habitat preferences. Larvae of both species were found together in several streams of moderate, steady flow (stations 15, 37, 43, and 57). A pair of *B. microscaphus* was observed in amplexus in fast-flowing water at 0905 on 3 May 1974 at station 10.

Adults were active at night; toads were twice



FIGURE 13. Riparian Woodland vegetation in Arroyo San Rafael at station 14.

observed far from water, in coastal sage scrub and chaparral. On three occasions, they were observed returning to riparian habitat at dawn.

Adults were collected at stations 14 (MVZ 140719), 43 (MVZ 140713, 140738), 49 (MVZ 140715–18, 147512), and 56 (MVZ 140714). Juveniles were collected or observed 13 July 1973 at station 57 (MVZ 140739) and 3 August 1973 at station 49. Larvae were observed 13 July 1973 at station 43 and 31 July 1973 at station 15.

Bufo punctatus Baird and Girard, 1852a,
Red-spotted Toad

I observed this toad in riparian habitats with flowing water at three localities on the East Scarp surrounded by rocky creosote bush scrub habitat. Three specimens are known from the Main Scarp at La Grulla (SU 12945–47). The species also is known from the Sierra Juárez (CAS 121201–09). Bostic (1971) reported the species in the Central Desert.

Adults were observed or collected at stations 17, 46 (MVZ 140720, 140747), and 60; juveniles were collected on 24 April 1974 at station 17 (MVZ 140748). Larvae were observed or col-

lected 14 April 1974 at station 46 (MVZ 140740) and 16 April 1974 at station 59. Larvae also were observed on 29 April 1974, 1 km above station 4.

Hylidae

Hyla cadaverina Cope, 1866,
California Treefrog

I found this frog in riparian woodland throughout the Sierra, but it was rare on the Main Scarp; the highest elevation recorded was 2,300 m. The species is common on the West and East scarps and in the arroyos of the Western Foothills. Adult males were heard chorusing at station 64, a spring in the North Central Desert. Duellman (1970) reported *Hyla cadaverina* from 32 km east of El Rosario. South of the Mártir Region, it is known from Bahía de Los Angeles (LACM 1305, 13163–69), 4.8 km N of Rancho Cataviña (LACM 13173–95), and from Rancho Santa Ynez (LACM 107923–26, 113730–31); these localities are the southernmost records for the species in Baja California.

These treefrogs were usually found among steep

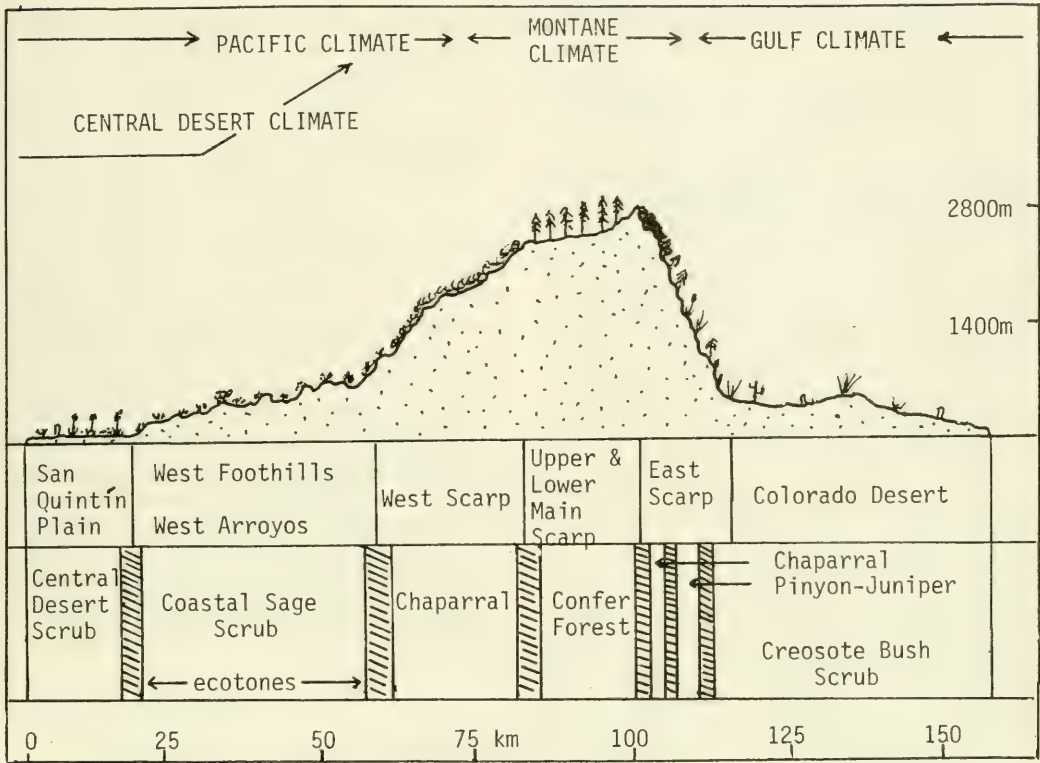


FIGURE 14. The ecogeographic formations of the Sierra San Pedro Mártir Region, Baja California Norte, México at latitude 31°N. An ecogeographic formation is comprised of a topographic element (Fig. 4), a climatic element(s) (Fig. 2c, Table 1), and a vegetation association (Fig. 5, Table 2). Riparian Woodland Associations are present within all vegetations and form the primary vegetation in the Western Arroyos. A ninth ecogeographic formation, the North Central Desert, occurs south of latitude 31°N; it is continuous with the San Quintín Plain Ecogeographic Formation and contains similar vegetation.

granitic boulders and cliff facings above fast-flowing water. Cunningham (1964) observed the aquatic garter snake, *Thamnophis hammondi*, eating this frog. The substrate preference of this frog may be related to the predatory habits of *T. hammondi*, which was twice observed attempting to climb streamside rock faces in the near vicinity of perched treefrogs. On two occasions I observed these frogs on sand, gravel, and aquatic vegetation at streamside. These localities were isolated riparian sites created by springs on the lower East Scarp; *T. hammondi* was not observed at these localities (above stations 4 and 46). Boulders and rock facings were present in riparian habitat at these localities.

Groups of 5–30 individuals were commonly observed congregating in direct sunlight in the mist above cataracts and waterfalls in the after-

noon. Individuals moved back and forth from shade to sunlight, perhaps for thermoregulation.

Adults were collected at station 35 (MVZ 140746), 41 (MVZ 140721), 49 (MVZ 140729–31), and 56 (MVZ 140722, 140724–25); they were observed at or near stations 4, 10, 16, 17, 20, 21, 23, 27, 46, 60, and 64. Juveniles were collected 13 July 1973 at station 56 (MVZ 140723); larvae were collected on 14 April 1974 at station 46 (MVZ 140741), and were observed through 29 April 1974 at stations 4, 16, 20, 21, 23, and 59.

Hyla regilla hypochondriaca Hallowell, 1854,
Pacific Treefrog

Hyla regilla hypochondriaca ranges to 2,750 m in riparian habitat in the coniferous forest,

and was found in the riparian woodland in the Arroyos of the West Scarp and Western Foothills, west to the Pacific coast. Bostic (1971) reported *H. r. deserticola* (= *hypochondriaca*) from two localities in the Central Desert.

All *Hyla regilla* were observed near standing and slow-flowing water. Most animals were in aquatic vegetation at streamside or floating in the water. *H. regilla* was rarely observed more than 15 cm above the ground or more than 1 m from water. This contrasts with *H. cadaverina*, which was found in areas of fast water flowing over granite boulders where the frogs inhabited rock surfaces often 2–5 m above the water. These two treefrog species seldom occurred in sympatry within the Region as a result of the unique riparian microhabitats occupied by each; I found them together at a single locality (station 27). *H. r. hypochondriaca* was active diurnally only under conditions of deep shade or cloud cover; most activity was observed at twilight and at night.

Adults were collected at stations 44 (MVZ 11142–56) and 62 (MVZ 140746), and observed at stations 11, 12, 14, 19, 27, 29, 35, 37, 38, 39, 57, and 62. In excess of several hundred juveniles were observed 4 July 1973 at station 39. Larvae were observed 27 July 1973 at station 12 and 11 April 1974 at station 29.

Ranidae

Rana aurora draytoni Baird and Girard, 1852a, California Red-legged Frog

This species was abundant on the Lower Main Scarp, in riparian woodland, and wet meadow habitats of the coniferous forest up to an elevation of 2,200 m. They also were found in Arroyos of the West Scarp and Western Foothills to the Pacific coast. Linsdale (1932) reported this species from San Ramón at the mouth of Rio Santo Domingo, which is apparently the southernmost record for the species in Baja California.

I observed *Rana aurora* basking and feeding during the day in streamside and aquatic vegetation associated with fast, slow, and standing water. It was not observed in rocky areas with cascading water. Most of the *R. aurora* were found near deep pools which were used for escape cover.

Adult specimens were collected at stations 38 (MVZ 140732) and 39 (MVZ 140733–35); animals were observed at stations 14, 27, 35, 37,

39, 42, 44, and 49. Larvae with well-developed legs were collected on 10 August 1973 at station 10 (MVZ 140736).

Rana boylii Baird, 1854,
Foothill Yellow-legged Frog

On several occasions I made extensive searches of the Lower Main Scarp near the western edge at La Grulla (station 39) where Loomis (1965) reported three specimens of *R. boylii*. I did not find this species here or along any other watersheds in the Sierra. The preferred habitat of *R. boylii*—fast-flowing water over gravel or cobble streambeds—is rare in the Mártir Region, and I suggest that *R. boylii* may be a marginal species in the Region as a result of habitat limitations. The abundance of *R. aurora* in montane riparian habitat may also contribute to the scarcity of *R. boylii*. Stream alterations due to mining activities and acid rain are other possible explanations for the scarcity or loss of this species from the Region.

TESTUDINATA

Emydidae

Clemmys marmorata (Baird and Girard, 1852a), Pacific Pond Turtle

Linsdale (1932) reported *Clemmys marmorata* from Valle de Trinidad (probably in Rio San Antonio) and Arroyo San Telmo, on the Pacific Slope. A record from 3.2 km south of Valladares (CAS 56884–85) placed the species in a third arroyo to the south. P. Haneline (pers. comm.) collected a specimen of *C. marmorata* from 30 mi east of El Rosario (Rancho El Metate, station 65). In May 1974, I was informed by the ranch foreman at this locality that this animal was brought from a more northern population. I found *C. marmorata* in the deep pools of a perennial stream at Rancho San Antonio on Arroyo Santo Domingo, at the base of the West Scarp (station 49). This site is the southern distribution limit; incongruously, giant cardon (*Pachycereus pringlei*) and barrel cactus (*Ferocactus* sp.) occur a few meters from streamside. This turtle is uncommon in the Mártir Region, probably as a result of alteration of riparian habitat for agricultural purposes.

Seeliger (1945) reported that the six specimens she examined from Baja California are not sim-

ilar to either described subspecies in California. Bury (1970) suggested that an analysis of geographic variation in this species is needed.

Five specimens were collected at station 49 (MVZ 207759–63). An adult turtle was seen diving in a pool on the West Scarp, at 1,600 m in Arroyo de San Rafael (station 10).

SAURIA

Gekkonidae

Coleonyx switaki (Murphy, 1974),
Barefoot Gecko

Fritts et al. (1982) reported *Coleonyx switaki* from eastern San Diego County, California and from Bahía de Los Angeles south of the Mártir Region. These and previous records (Murphy 1974) and the ecological preferences noted by Fritts et al. (1982) suggest a contiguous range for this gecko along the eastern flank of the Peninsular Range Mountains, although no specimens have been reported from the Mártir Region.

Coleonyx variegatus variegatus (Baird, 1859),
Desert Banded Gecko

Coleonyx variegatus abbotti Klauber, 1945,
San Diego Banded Gecko

The Desert Banded Gecko, *Coleonyx variegatus variegatus*, occurs in the Colorado Desert and south to San Felipe (Klauber 1945). A single specimen from the vicinity of Bahía de Los Angeles (CAS 121182) appears to be *C. v. peninsularis* Klauber (A. Leviton, pers. comm.). This specimen is apparently an unreported northern range extension for the subspecies on the Gulf Slope.

Coleonyx variegatus abbotti Klauber, the San Diego Banded Gecko, occurs on the Pacific Slope of the Mártir Region. This lizard was collected at Rancho San José (SDNHM 24390) and east of San Telmo (SDNHM 42542) in the Western Foothills; Bostic (1971) reported two specimens from the Central Desert.

I collected two specimens of *Coleonyx variegatus variegatus* in Valle de San Felipe near the east side of San Matías Pass (MVZ 140742–43). These specimens resembled *C. v. variegatus* (Klauber 1945) except that they had a clear and distinct nuchal light loop, characteristic of *C. v. abbotti*. Klauber (1945) postulated that these races intergrade across some low passes in the Pen-

insular Range, and the present specimens support this contention.

Phyllodactylus nocticolus (Dixon, 1964),
Baja California Leaf-toed Gecko

Dixon (1969) indicated that *Phyllodactylus nocticolus* ranges along the east scarps of the Peninsular Range from California southward down the length of Baja California. He noted that *P. n. nocticolus* occurs through the Mártir Region. Bostic (1971) described a new subspecies, *P. n. sloani*, from the Central Desert, thus extending the species range to the Pacific Slope, south of the Mártir Region. The northernmost locality he reported was 39 km SE Rosario (29°48'N, 115°33'W).

I collected two specimens of *Phyllodactylus nocticolus* at station 65 (MVZ 140744–45) about 25 km NW of the above locality. This site is a volcanic slope with boulders, in Central Desert scrub vegetation. The geckos were both under exfoliating slabs of volcanic rock, 1.3 m above ground. These two specimens had 21 paravertebral tubercles, within the range of both *P. n. nocticolus* and *P. n. sloani*, but only 28 and 30 longitudinal rows, within the range of *P. n. nocticolus* and below that of *P. n. sloani* (Dixon 1964; Bostic 1971).

Iguanidae

Callisaurus draconoides Blainville, 1835,
Zebra-tailed Lizard

Callisaurus draconoides occurs on both Gulf and Pacific slopes of the Mártir Region. It inhabits all scrub vegetations, and is most abundant in the creosote bush scrub of Valle de San Felipe and Valle Chico. It ranges through San Matías Pass into Valle de Trinidad (SDNHM 16869–81), and occurs at Rancho San José (Linsdale 1932), and 16 km west of station 10 in the Western Foothills. *C. draconoides* is uncommon, with a spotty distribution on the Pacific Slope of the Region; distribution and abundance increase southward into the Central Desert (stations 63, 64; Bostic 1971). North of the Region, it occurs at Punta Banda (LACM 94409) and east of Ensenada (LACM 107136).

This species was found in sandy areas of open benches and slopes, or on sandy soil around scattered outcrops. Specimens were collected at sta-

tions 2 (MVZ 140753), 4 (140750–51), and 63 (MVZ 140752); animals were observed at stations 1, 5, 46, 54, 61, 64, and 65.

Crotaphytus insularis vestigium

Smith and Tanner, 1972,

Baja California Black-collared Lizard

Smith and Tanner (1972) described *Crotaphytus insularis vestigium* and indicated a Gulf Slope range for the species through south central Baja California. It is known from the lower East Scarp of the Mártir Region (SU 17048; Linsdale 1932).

I collected two adult males at stations 49 (MVZ 140754) and 65 (MVZ 140755), on the Pacific Slope of the Region. These records confirm the validity of two unreported, and apparently ignored, specimens collected in 1935 from Rancho San José (station 27; SDNHM 24391–92). Van Denburgh (1922) reported this species at Trinidad, west of San Matías Pass, the northernmost record on the Pacific Slope. The lizard is now known from the Mártir Region, from the Pacific Slope of the Central Desert at Mesa de San Carlos (Bostic 1971), and near Rancho Cataviñá (LACM 16993, 63176). In Baja California Sur, it occurs at Arroyo La Purísima, 12.8 km southwest of Canipolé (SU 11545); 4.0 km northeast San José de Comondú; at Comondú; at La Purísima; and 9.6 km and 52.8 km north of Canipolé (Smith and Holland 1971). These records indicate a much greater distribution for this lizard in Baja California than the Gulf Slope range proposed by Smith and Tanner (1972, 1974).

Both specimens I collected were basking on boulders during the midafternoon. The site at station 65 is a rocky volcanic slope grown to Central Desert scrub; the site at station 49 is a granite outcrop in coastal sage scrub.

Dipsosaurus dorsalis dorsalis

Baird and Girard, 1852a,

Desert Iguana

This lizard is known from numerous localities in the Colorado Desert, south to Bahía de Los Angeles on the Gulf Slope (Murray 1955). Linsdale (1932) reported it from the Vizcaíno Desert near San Ignacio. A second race is recognized south of the Vizcaíno Desert through the Cape Region (Schmidt 1922). The species is absent from the Pacific Slope of Baja California north of latitude 29°N in the Central Desert Region.

I observed *Dipsosaurus dorsalis dorsalis* along the base of the East Scarp in Valle de San Felipe and Valle Chico (stations 5 and 54), and in a canyon bottom west of the scarp base (station 61). All observations of *D. d. dorsalis* occurred in creosote bush scrub on open benches and slopes with a sandy substrate.

Gambelia wizlizenii copei (Yarrow, 1882),

Cope's Leopard Lizard

Gambelia wizlizenii wizlizenii

(Baird and Girard, 1852b),

Longnose Leopard Lizard

Banta and Tanner (1968) indicated that *Gambelia wizlizenii copei* occupies most of the peninsula south of the Mártir Region, ranging north to the vicinity of San Felipe on the Gulf coast, and that *G. w. wizlizenii* occurs in the Colorado Desert of northeastern Baja, from the vicinity of San Felipe northward. On the Pacific Slope, *G. w. copei* ranges on the coast to just north of the Mártir Region and inland north just into the United States (Banta and Tanner 1968; Mahrdr 1973).

I collected four specimens of *Gambelia wizlizenii copei* on the Pacific Slope of the Mártir Region. I found two active males during mid-morning at station 27 (MVZ 140756–57). They were on sandy soil under shrubs in an area of scattered granite outcrops, in coastal sage scrub. A third adult male was captured basking on a rock in creosote bush scrub at station 2 (MVZ 140759). A subadult female was captured emerging from a burrow at 0815 hr in coastal sage scrub/oak woodland ecotone at the head of Arroyo San Telmo (1,480 m elevation), station 19 (MVZ 140758). I observed one probable *G. w. copei* on the lower East Scarp in creosote bush scrub at station 46.

Petrosaurus mearnsi (Stejneger, 1894),

Banded Rock Lizard

This species has been reported from numerous East Scarp localities (Van Denburgh 1922; Linsdale 1932). It ranges south on the Gulf Slope to Bahía de Los Angeles (CAS 85338), and occurs north into California as far as Riverside County. *Petrosaurus* is absent from the Pacific Slope north of the Central Desert region.

I observed *Petrosaurus mearnsi* only in rocky

areas of both creosote bush scrub and pinyon-juniper woodland up to 1,220 m. Few individuals were seen on the ground as *P. mearnsi* seems to prefer steep rock faces from 1.5 to 5.0 m above ground. The angles of slope of perching sites measured for *P. mearnsi* were greater than those of all other species of lizards in the Region, commonly exceeding 90°. These lizards were active all day, with a midmorning peak. The greatest densities of lizards were at riparian edges in canyons of the East Scarp.

Specimens were collected at stations 17 (MVZ 140762) and 59 (MVZ 140760–61). I observed *P. mearnsi* at stations 4, 16, 20, 21, 23, 46, 48, 59, 60, and 61.

Phrynosoma coronatum (Blainville, 1835),
Coast Horned Lizard

Reeve (1952) indicated that the race *Phrynosoma coronatum schmidtii* occurs on the Pacific Slope of the Mártir Region, south into the Central Desert, and northward to near the United States border. Bostic (1971) reported the species from the Central Desert, but he did not indicate subspecific affinities. *P. coronatum* appears to be absent on the Gulf Slope north of latitude 29°N.

I observed lizards in chaparral up to 1,400 m at station 18, and at many localities in coastal sage scrub. They frequented sand, soil, and rock rubble substrates. *P. coronatum* was active in direct sunlight and on substrates with unusually high surface temperatures (up to 49°C), when other lizard species were relatively inactive and seeking shelter in shade.

Specimens were collected at stations 10 (MVZ 140824), 18 (MVZ 140826), 27 (MVZ 140823, 140825), 28 (MVZ 140821), and 49 (140822).

Phrynosoma mcallii (Hallowell, 1852),
Flat-tailed Horned Lizard

Reeve (1952) reported three specimens of *Phrynosoma mcallii* from extreme northeastern Baja California (Colorado Desert). One record exists from further south, at the mouth of Guadalupe Canyon, at the foot of the Sierra Juárez (CAS 119077). This species has yet to be reported from the desert immediately east of the Sierra San Pedro Mártir. *P. mcallii* occurs in the vicinity of sand dunes and sandy flats (Stebbins 1985); such habitat is present in the Mártir Region, but is not continuous with similar habitat to the north.

Phrynosoma platyrhinos calidiarum (Cope, 1896),
Southern Desert Horned Lizard

Reeve (1952) reported seven records for *Phrynosoma platyrhinos calidiarum* in northeastern Baja California, four from the South Colorado Desert in the vicinity of San Felipe. Welsh and Bury (1984) reported it from three localities inland from the Gulf. Other records of note include: Valle de San Felipe (station 5; SU 18588), Montes de Media (SDNHM 25252), and 15 km north of Bahía de San Luis Gonzaga (CAS 91631). *P. platyrhinos* may occur south to the vicinity of Bahía de Los Angeles. Apparently it is absent on the Pacific Slope of the Mártir Region and in the Central Desert.

Sauromalus obesus obesus (Baird, 1859),
Western Chuckwalla

Gates (1968) first reported *Sauromalus obesus* in northern Baja California from specimens collected at six localities on the Gulf Slope. The northernmost locality was San Matías Pass (station 1); the southernmost record was 36 km southwest of Bahía de San Luis Gonzaga. I collected an adult female at station 16 (MVZ 140749) and observed individuals at stations 17 and 46 on the east scarp. Apparently this species is absent on the Pacific Slope of the Region.

Recent records from about 5 km north of Punta Prieta (MVZ 117420 and 117467–69) extend the known range of *S. obesus* south into the Central Desert. A single record from the Sierra Juárez at Cañón Cantillas (SDNHM 43974) fills some of the gap between Baja California populations and those known from southern California. This saxicolous species probably occurs throughout the east scarps of the Peninsular Range from California into the Central Desert of Baja California. Bostic (1971) reported *S. australis* from 50 km south of Punta Prieta in the Central Desert, thus indicating that a zone of sympatry between *S. australis* and *S. obesus* probably exists in the Central Desert in the vicinity of Punta Prieta. Seib (1980) implies that this zone of sympatry does not exist in the Central Desert, ignoring *S. australis* and treating all populations in the Central Desert as *S. obesus*. More work is needed to clarify relationships among the chuckwallas of Baja California.

Sauromalus obesus was unusually wary in the Mártir Region. Individuals sought cover in re-

sponse to movement at distances as great as 70 m. The lizards occurred on high cliff faces and ledges, and seldom ventured far from crevices where they sought cover. These large dark lizards contrast greatly with the pale granite surface of the Mártir Region. The wariness of *S. obesus* may allow use of these pale surfaces in an area with high densities of raptorial birds (Short and Crossin 1967). I submit that the dark color may be a thermoregulatory adaptation, which has a higher selective value than does cryptic coloration for predator avoidance. The extreme wariness of *S. obesus* may explain why this species remained unreported for so long in this area.

The specimen captured 12 June 1974 at station 16 contained six well-developed ova. Scutellation most closely matched the description for the race *Sauromalus obesus obesus* (Shaw 1945).

Sceloporus graciosus vandenburghianus
Cope, 1896,
Southern Sagebrush Lizard

This lizard was the most frequently observed reptile on the Main Scarp of the Sierra. Its distribution was limited to coniferous forest, conifer-chaparral ecotone, and related riparian edge habitats of the upper scarps, from 1,980 to 2,820 m. Lizards were active from 0500 to 1800 hr on boulders, logs, and occasionally on the forest floor; juveniles occurred mostly on the ground. In the Mártir Region, *Sceloporus graciosus vandenburghianus* exhibited frequent climbing behavior. Elsewhere, they are found mostly on the ground (Stebbins 1966).

The distribution of *S. graciosus* in the Mártir Region may be influenced by interspecific competition. I expected it to exist in the chaparral of the East and West scarps of the Region, a seemingly appropriate habitat. In fact, I found it in stands of open chaparral only above 2,100 m on the Main Scarp. The closely related *S. occidentalis* occurs in chaparral on the East, West, and Main scarps below 2,100 m. This suggests that *S. occidentalis* may be limited to lower areas with higher temperatures, whereas *S. graciosus* is found in cooler climes above 2,100 m. The mechanism of exclusion could be simple aggressive dominance of the larger species (*S. occidentalis*) over the smaller (*S. graciosus*), driving the latter away from critical resources at lower elevations (interference competition). Feeding

strategies may also play a role in segregating these two lizards. In the ecotonal vegetation between 1,970 and 2,100 m where these two lizards co-exist, limited observations indicated a difference in their choice of perching and foraging sites. Adult *S. graciosus* were most often on elevated perches and descended to forage on the ground. *S. occidentalis* was always observed on the ground or on low boulders.

Specimens were collected at stations 8 (MVZ 140773–74), 25 (MVZ 140763), 38 (MVZ 140768–69, 147514), 39 (MVZ 140764–67, 147513), 47 (MVZ 140770–71), 55 (MVZ 140772), and 58 (MVZ 140785–86); observations were made at stations 12, 22, 24, 25, 30, 32, 36, 37, 42, 44, 47, and 55.

Sceloporus magister rufidorsum Yarrow, 1883,
Red-backed Spiny Lizard

Sceloporus magister uniformis
Phelan and Brattstrom, 1955,
Yellowback Spiny Lizard

Phelan and Brattstrom (1955) reported four subspecies of *Sceloporus magister* in Baja California. Hall (1973) indicated that these taxa can be divided into two distinct karyological groups indicating at least two, and possibly four, distinct species. Murphy (1983a), citing Hall and unpublished electrophoretic data, treated the forms as separate species. I reserve judgement until more information is available, treating the northern forms as subspecies. Two forms, one from each karyological group, occur in the Mártir Region: *S. m. uniformis* ($2n = 26$ chromosomes) in the Colorado Desert south to San Felipe on the Gulf Slope and *S. m. rufidorsum* ($2n = 30$ chromosomes) on the Pacific Slope, from just north of the Mártir Region south through the Central Desert. Subspecific morphological differences are primarily based on dorsal pattern and coloration of adult males, with the number of femoral pores as a secondary distinguishing character (Phelan and Brattstrom 1955).

I collected three adult males. A male from station 2 (MVZ 140799) had a uniform beige dorsum and a femoral pore count of 13-13, which closely matches the description of *S. m. uniformis*. An adult female from station 2 (MVZ 140798) also fits this description. The other males, collected at station 27 (MVZ 140793–94) were not similar to the described forms (Phelan and

Brattstrom 1955). These two males had a faint and diffuse rust color dorsally, and lacked any pattern or side bars. Femoral pore counts were 17-18 and 16-16, which corresponds to *S. m. rufidorsum* (15-20), not to *S. m. uniformis* (10-15). Other specimens of the *S. magister* complex collected were an adult female from station 62 (MVZ 140797), and three juveniles, two males, and one female from station 64 (MVZ 140795-96, 147517). All of these matched the description for *S. m. rufidorsum*.

This small sample suggests the possibility of integration between two forms occurring in the Mártir Region. Similarly, Bostic (1971) examined 13 males from the Central Desert and found only one specimen with a typical *Sceloporus magister rufidorsum* pattern. Further biochemical work is needed to describe variation in the *S. magister* complex in this part of Baja California.

Sceloporus magister was observed in all scrub vegetation on both the Gulf and Pacific slopes of the Mártir Region, up to 1,220 m, and south into the Central Desert. It was usually seen in association with plant forms that afforded protective cover. Lizard burrows were located at the base of plant species such as Mojave Yucca (*Yucca schidigera*), *Agave* sp., and Cholla (*Opuntia* sp.). Lizards often were observed up to 1.5 m above ground in a wide variety of woody plants. I saw *S. magister* in all regional edaphic types, including riparian edge, and on all substrates. *S. magister* was observed at stations 5, 9, 10, 16, 18, 63, and 65.

Sceloporus occidentalis biseriatus

Hallowell, 1854,

Great Basin Fence Lizard

This lizard reaches its southern limit in the Mártir Region, where it occurs primarily along the Pacific Slope. It was abundant in the chaparral of the West and Upper East scarps, and uncommon in conifer-chaparral ecotones on the Lower Main Scarp (stations 43 and 47). This species was absent above 2,120 m. On the lower Pacific Slope, in areas of coastal sage scrub, it was found only in riparian habitat.

In riparian woodland, *Sceloporus occidentalis* was highly arboreal, commonly found 1.5 m or more above ground on trees and fenceposts. Lizards foraged on the ground from these elevated perches; when startled, they returned to their

perches. In the chaparral and conifer-chaparral ecotone, *S. occidentalis* was primarily ground-dwelling. In the conifer-chaparral ecotone, *S. occidentalis* is sympatric with *S. graciosus* (see above).

Specimens were collected at stations 10 (MVZ 140790), 19 (MVZ 140792, 147518), 27 (MVZ 140791), 29 (MVZ 140788), 35 (MVZ 140789), 43 (MVZ 140781), 47 (MVZ 140782-83), 53 (MVZ 140784), 55 (MVZ 140787, 147515), and 58 (MVZ 140785-86); observations were at stations 14, 19, 56, and 57.

Sceloporus orcutti Stejneger, 1893a, Granite Spiny Lizard

Sceloporus orcutti occurs on the rocky scarps of the Mártir Region in scrub vegetations, pinyon-juniper woodland, and chaparral. It reaches the conifer-chaparral ecotone on the Lower Main Scarp (station 39) at 2,080 m. It is most abundant on the lower East Scarp in rocky creosote bush scrub. This species is entirely saxicolous, and is associated with large boulders, outcrops, or rock faces.

Sceloporus orcutti was extremely wary and difficult to approach, reacting to my presence at a distance of about 30-40 m. I observed one lizard taken by a Harris' Hawk (*Parabuteo unicinctus*) and another by a Red-tailed Hawk (*Buteo jamaicensis*). The abundance of large raptorial birds in the Mártir Region, the dark body color of this spiny lizard, and the pale granite surfaces frequented by this species may together explain the extreme wariness displayed by *S. orcutti*. Mayhew (1963) mentioned this wariness and noted a southward increase in its intensity. *S. orcutti* is easily captured by noose at the north end of its range in the San Jacinto Mountains of California, but it becomes increasingly difficult to approach further southward, and is virtually impossible to noose in the Mártir Region. *Buteo* populations at the northern extreme of this lizard's range may be less dense, due to human interference, or there may be a greater choice of prey animals to select from. Both factors would result in less intense selective pressure for alertness in *S. orcutti*.

Sceloporus orcutti was collected at stations 17 (MVZ 140776-78), 27 (MVZ 140779, 147516), 46 (MVZ 140775), and 65 (MVZ 140780); observations were made at stations 2, 4, 10, 11, 14, 29, 35, 37, 39, 48, 49, 51, 56, 59, 60, and 62.

Uma notata notata Baird, 1859,
Desert Fringe-toed Lizard

Schmidt (1922) noted two records for *Uma notata notata* from the desert east of the Sierra Juárez, approximately 160 km north of the Mártir Region. Norris (1958) suggested this arenicolous lizard is restricted to contiguous sand dune habitat, which may explain its apparent exclusion from the Mártir Region, where dune habitat is not contiguous. On the other hand, the lack of records for *U. notata* may be an artifact of limited collecting.

Urosaurus graciosus graciosus Hallowell, 1854,
Western Brush Lizard

Urosaurus graciosus graciosus is known from the South Colorado Desert at San Felipe (Linsdale 1932); it ranges northward through the deserts of California and Arizona. Stebbins (1966) indicated that *U. g. graciosus* ranges through much of northeastern Baja California. I collected two adult males in creosote bush scrub at the base of the East Scarp, one in Valle Chico (station 61) (MVZ 140808), and the other in Valle de San Felipe near station 17 (MVZ 140809). Both specimens were 1–2 m above ground in ironwood trees (*Olneya tesota*). These localities extend the known range of this species slightly south and east.

Urosaurus graciosus graciosus is absent from the East Scarp and the Pacific Slope of the Mártir Region, and is also unknown from the Central Desert. *U. microscutatus* and *U. lahtelai* occur in these respective areas (see below and Rau and Loomis 1977); presence of these congeners may exclude *U. g. graciosus*.

Urosaurus microscutatus (Van Denburgh, 1894),
Small-scaled Lizard

Urosaurus microscutatus was common on the rocky scarps of the Mártir Region in all scrub vegetations, chaparral, and pinyon–juniper woodland; it occurs up to 2,120 m on the East Scarp, and 1,525 m on the West Scarp. The species is not present on open sandy desert and areas with few outcrops; it is absent in the South Colorado Desert and San Quintín Plain, and uncommon in the Western Foothills. Bostic (1971) reported it as uncommon in the Central Desert.

This species is arboreal, occurring up to 2.5 m above ground. It commonly descends from ele-

vated perches to forage on the ground. I found *Urosaurus microscutatus* on boulders and in vegetation, with females and young occasionally observed on the ground. Greatest densities were reached in the rocky creosote bush scrub areas of the East Scarp along the riparian edge.

Specimens were collected at stations 10 (MVZ 140814, 140819), 27 (MVZ 140820), 46 (MVZ 140815–16, 147519), 49 (MVZ 140812–13), 51 (MVZ 140811), 53 (MVZ 140810, 147520), and 59 (MVZ 140817–18); observations were made at stations 4, 11, 17, 19, 23, 48, 60, 61, 62, and 65.

Uta stansburiana elegans (Yarrow, 1883),
California Side-blotched Lizard

Ballinger and Tinkle (1972) indicated that a single race of the Side-blotched Lizard occurs throughout peninsular Baja California. This species is the most common and ubiquitous lizard in the Mártir Region at all elevations and in all vegetations except coniferous forest. On the Lower Main Scarp it ranges up to 2,120 m in chaparral.

Uta stansburiana elegans showed no special edaphic or substrate preference. It is mostly a ground lizard but occasionally occurs up to 1.5 m above ground on rock outcrops.

Specimens were collected at stations 10 (MVZ 140806), 27 (MVZ 140807), 35 (MVZ 140802), 45 (MVZ 140803), 46 (MVZ 140805), 49 (MVZ 140804, 147522), 54 (MVZ 140800, 147521), and 56 (MVZ 140801); observations were made at stations 1, 2, 4, 9, 14, 17, 19, 47, 48, 57, 59, 60, 61, 62, 63, 64, and 65.

Xantusiidae

Xantusia henshawi henshawi Stejneger, 1893b,
Granite Night Lizard

This saxicolous species occurs on all the rocky scarps of the Sierra San Pedro Mártir, up into the coniferous forest on the Lower Main Scarp at Arroyo Encantada (2,100 m; CAS 57294–96), and the conifer–chaparral ecotone at La Grulla (station 39; Murray 1955). I collected a specimen in chaparral at station 19 (MVZ 140828), and three specimens in coastal sage scrub at station 27 (MVZ 140827–28, 140830). I saw one on the East Scarp in pinyon–juniper woodland at station 51. The species undoubtedly occurs to the desert floor at the base of the East Scarp (Stebbins

1966; Lee 1975) but its secretive habits and the ideal protective habitat of the cliffs and canyons on the East Scarp make collecting difficult. All animals were found under exfoliating slabs on large granite boulders. The species is as yet unreported in the Central Desert, possibly because of the marked change in geomorphology that occurs at this latitude. The primarily granitic formations that dominate in the Mártir Region and provide cover for this species give way to volcanic formations in the Central Desert.

Xantusia vigilis vigilis Baird, 1858,
Desert Night Lizard

Xantusia vigilis wigginsi Savage, 1952,
Baja California Night Lizard

This lizard occurred most commonly in areas of open benches and slopes in creosote bush and Central Desert scrub on both the Gulf and Pacific slopes. Apparently it is absent in the coastal sage scrub of the Western Foothills. I collected one specimen on the rocky lower West Scarp at 1,400 m in pinyon-juniper woodland (station 10; MVZ 140833).

Savage (1952) indicated that the Mártir Region was the probable area of intergradation between the races *Xantusia vigilis wigginsi* of central Baja California, and *X. v. vigilis* of the southwestern United States. Two adult males from San Matías Pass (station 1) matched Savage's description of *X. v. wigginsi* on the basis of tail pattern, but showed a dorsal pattern found in both forms. A juvenile from station 1 had dorsal characteristics of *X. v. vigilis*. An adult from station 10 completely lacked a pattern, and did not fit any previous descriptions. A juvenile from the South Colorado Desert near station 54 had the dorsal pattern of *X. v. vigilis* and the tail pattern of *X. v. wigginsi*. One of each of two juveniles from station 62 in the north Central Desert fits closely the descriptions of *X. v. wigginsi* and *X. v. vigilis*. A series of specimens attributed to *X. v. wigginsi* (SDNHM 41340–52), was collected at San Telmo, a lowland locality of the Pacific Slope dominated by Central Desert scrub. The eight specimens I collected show characteristics of both subspecies, and failed to match either satisfactorily. These findings support Savage's speculation of intergradation in this Region.

All animals I collected were taken from rubble

and dead fall of Mojave yucca (*Agave* sp.), barrel cactus, or *Echinocactus* sp. Specimens were collected at stations 1 (MVZ 140831, 147523), 2 (MVZ 140836–37), 10 (MVZ 140833), 54 (MVZ 140832), 64 (MVZ 140834–35); observations were recorded at stations 14 and 65.

Scincidae

Eumeces gilberti rubricaudatus Taylor, 1935,
Western Redtail Skink

Jones (1985) indicated that *Eumeces gilberti rubricaudatus* ranges south to the Sierra San Pedro Mártir in Baja California, but with an inland distribution. Rogers and Fitch (1947) reported *E. g. rubricaudatus* from the Pacific coast of the Mártir Region at San Antonio del Mar (station 9). A record from La Grulla (station 40; SDNHM 44291) indicates that they range into the coniferous forest-chaparral ecotone. I collected three specimens, from stations 14 (MVZ 140842), 27 (MVZ 140843), and 49 (MVZ 140841) and observed one at station 19. All were in deep riparian woodland; light intensity range 50–85 FC, relative humidity 33–41% (Welsh 1976a). Jones (1985) reported this species in the chaparral vegetation of the Mártir Region but failed to cite specimens, suggesting this may be an assumption based on habitat associations observed elsewhere. Evidence to date suggests that this species is restricted to the riparian corridors in the Region, and may occur along the moist coastal corridor of the San Quintín Plain. A record from Guadalupe Canyon in the Sierra Juárez (CAS 119087) suggests it may also occur in riparian vegetation on the East Scarp of the Mártir Region.

Eumeces skiltonianus skiltonianus
(Baird and Girard, 1852b),
Western Skink

This lizard is common in the coniferous forest of the Sierra, occurring up to 2,800 m (station 22). It also occurs on the West Scarp and at lower elevations on the Pacific Slope; records include Rancho San José (Linsdale 1932) and 6.6 km east of San Telmo (SDNHM 42741). Coastal records for *Eumeces skiltonianus* in the Mártir Region include: San Antonio del Mar (SDNHM 41990), 10 km southeast Punta Colnett (CAS 57556), San Quintín (CAS 55802), and Colonia Guerrero (LACM 107935).

On the lower Pacific Slope, in areas dominated by scrub vegetation, *Eumeces skiltonianus* appeared to be restricted to riparian habitat and the moist coastal corridor. Limited observations suggest this lizard reaches greatest densities in areas of riparian edge habitat.

Specimens were collected at stations 37 (MVZ 140838), 39 (MVZ 140839, 147524), and 50 (MVZ 140840). Sightings occurred at stations 10, 19, 22, and 38.

A site recorded from Cataviñá in the north Central Desert has recently come to my attention (D. Schmoldt, pers. comm. and 35-mm slide). This would constitute a new southern record for the subspecies if confirmed by a specimen.

Teiidae

Cnemidophorus hyperythrus schmidtii
(Van Denburgh and Slevin, 1921),
Orangethroat Whiptail

Cnemidophorus hyperythrus schmidtii occurs on the Pacific Slope from San Diego County, California, south through the Central Desert, where it ranges across to the Gulf coast, and through the Cape Region (Burt 1931). In the Mártir Region these whiptails were found in scrub vegetation of the western foothills and north Central Desert. Bostic (1968) found *C. hyperythrus* on the San Quintín Plain, but he considered habitat there to be suboptimal; *C. labialis* was far more abundant than *C. hyperythrus* in this area.

I found *Cnemidophorus hyperythrus* to be terrestrial and diurnal, showing preference for areas of fine-textured, soft soils with shrub cover. It was most abundant in riparian/scrub ecotone. I saw American Kestrels (*Falco sparverius*) capture individuals of *C. hyperythrus* on two occasions. Specimens were collected at stations 27 (MVZ 147525), 49 (MVZ 140844–46), 62 (MVZ 140849–50), and 64 (MVZ 140847–48).

Three subspecies of *Cnemidophorus hyperythrus* have been described from Baja California: *C. h. hyperythrus*, *C. h. schmidtii*, and *C. h. beldingi* (Linsdale 1932). The northern race, *C. h. beldingi*, is generally distinguished by the presence of two middorsal stripes that are lacking in the central race, *C. h. schmidtii* (Murray 1955). Murray noted a difference between races in the number of supraoculars that were separated by granules from the frontals, which he considered a more diagnostic character. Bostic (1971) de-

scribed 15 specimens from the Central Desert, the presumed range of *C. h. schmidtii*, that match Murray's characters for *C. h. beldingi*.

The eight specimens I collected appear to be of the race *C. h. schmidtii*. Available data (Table 3) indicate only slight differences between the subspecies. I suggest that there is insufficient differentiation to warrant three distinct races. With most morphological characters showing a north to south clinal variation, I consider the central peninsular region to be an area of intergradation for the ecotypes *C. h. beldingi* and *C. h. hyperythrus*. Burt (1931) recognized no subspecies.

Cnemidophorus labialis Stejneger, 1890,
Baja California Whiptail

Cnemidophorus labialis is endemic to north central Baja California, occurring primarily along the San Quintín Plain and the Pacific coast of the Central Desert Region. The northernmost record for *C. labialis* is Punta San José, about 40 km NW San Vicente (Bostic 1968). It ranges southward in the Central Desert to the vicinity of latitude 28°13'N. Bostic (1971) considered this to be near the southern limit of distribution. Vegetation in the range of *C. labialis* on the San Quintín Plain most closely approximates Central Desert scrub, with plant density increased and species composition altered slightly by the fog and cool, moist air. I did not collect any specimens of *C. labialis*.

Cnemidophorus tigris multiscutatus Cope, 1892a,
Coastal Whiptail

Cnemidophorus tigris tigris
Baird and Girard, 1852a,
Great Basin Whiptail

Cnemidophorus tigris multiscutatus occurs up to 1,980 m in the Mártir Region, on both sides of the peninsular divide in all types of scrub vegetation, pinyon-juniper woodland, and chaparral. It ranges to the coast on the Pacific Slope and south through the Central Desert (Bostic 1971). On the Gulf Slope, *C. t. multiscutatus* occurs in the south Colorado Desert in Valle de San Felipe and Valle Chico, along the base of the East Scarp. Murray (1955) collected the Great Basin Whiptail (*C. t. tigris*) from three Gulf coastal localities in the South Colorado Desert near San Felipe.

I found *Cnemidophorus tigris multiscutatus* only at ground level on sand, soil, rock, rubble,

TABLE 3. VARIATION IN MORPHOLOGICAL CHARACTERS AMONG SUBSPECIES OF *CNEMIDOPHORUS HYPERYTHRUS*. (See footnotes for sources of published data.)

Character	Subspecies			Mártir specimens	
	<i>beldingi</i>	<i>schmidti</i>	<i>hyperythrus</i>		
Number of granules around midbody	72.8 ± 0.8 (66–79) 17 ¹	75.2 ± 0.6 (66–83) 54 ²	77.6 ± 0.6 (69–90) 45 ¹	75.0 (70–80) 8	
Anterior supraoculars separated from the frontal by granules:					
only part of third	5 ³	10 ⁴	19 ²	28 ⁵	0
all of third	0	48 ⁴	14 ²	44 ⁵	8
only part of second	25 ³	3 ⁴	16 ²	4 ⁵	—
all of second	36 ³	15 ²	0	—	—
Number of middorsal lines:					
three	9 ⁶	0	48 ⁴	1	
two	104 ⁶	2 ⁴	3 ²	15 ⁴	2
one (forked anteriorly)	46 ⁶	59 ⁴	56 ²	3 ⁴	5

¹ Data from Walker and Taylor (1968).
² Data from Bostic (1971).
³ Data from Van Denburgh (1922).
⁴ Data from Linsdale (1932).
⁵ Combined data from Murray (1955) and Linsdale (1932).
⁶ Data from Burt (1931).

or leaf litter. I observed it foraging throughout the day, mostly in the broken shade of the shrub understory. When startled or chased, these whip-tails sought shelter in burrows.

Specimens were collected at stations 2 (MVZ 140857), 14 (MVZ 140854), 27 (MVZ 140855), 48 (MVZ 140853), 49 (MVZ 140852, 147526), 56 (MVZ 140851), and 62 (MVZ 140856, 147527). These animals resembled Bostic's (1971) collection of *Cnemidophorus tigris multiscutatus* from the Central Desert. *C. t. multiscutatus* was observed at stations 4, 5, 10, 17, 18, 19, 35, 46, 48, 49, 52, 57, 59, 60, 61, 62, 63, 64, and 65.

Anguidae

Elgaria multicarinata webbi (Baird, 1858),
San Diego Alligator Lizard

Elgaria multicarinata webbi is known from coniferous forest areas on the Lower Main Scarp at La Grulla (Linsdale 1932), Arroyo Encantada (CAS 57038–42), El Alcatraz (CAS 57330), and at station 37. This lizard was found in chaparral on the West Scarp at stations 10 (MVZ 140860) and 35 (MVZ 140859) and on the East Scarp at station 53 (MVZ 140858). Western Foothills records include: Valladares (Linsdale 1932); Mesquite Spring, Valle de Trinidad (SDNHM 16864); and Rancho San José (Linsdale 1932). These Western Foothill records are all from sites con-

taining riparian habitat. The chaparral habitat occupied by *E. m. webbi* at higher elevations is scarce below 1,220 m in the Western Foothills, and I suspect that its distribution below 1,220 m is localized primarily around the riparian corridors. Records from Cañón del Diablo (SU 17293–95) and Cañón El Cajón (Linsdale 1932) indicate a possible similar riparian distribution of *E. m. webbi* on the East Scarp below the chaparral association. Coastally, on the San Quintín Plain, I observed this lizard in Central Desert scrub at 1.7 km east of San Antonio del Mar (station 9), and it is also known from Colonia Guerrero (LACM 75501, 107933). Bostic (1971) indicated that this race occurs along the moist coastal belt of the Central Desert Region.

All specimens I collected were in areas of rocky outcrops, on granitic sand, soil, or rock rubble, except the individual near station 9, which was on open sandy ground near vegetation.

Anniellidae

Anniella geronimensis Shaw, 1940,
Baja California Legless Lizard

Anniella geronimensis occurs coastally on the San Quintín Plain from Colonia Guerrero south to the vicinity of El Rosario (Shaw 1953; Bezy et al. 1977). This species is endemic to the Mártir Region and a single near-shore island. Shaw

(1953) reported *A. geronimensis* sympatric with *A. pulchra* in the vicinity of Colonia Guerrero.

Anniella pulchra Gray, 1852,
Silvery Legless Lizard

Anniella pulchra occurs on the Pacific Slope within the Mártir Region at San José (SDNHM 40394), Socorro (SDNHM 8842), east of San Telmo (SDNHM 42738), San Antonio del Mar (SDNHM 4900–10), and west of Colonia Guerrero (Bezy et al. 1977). A resident told me that *A. pulchra* occurred in sandy fields at the bottom of the arroyo at station 19. This site at 1,450 m may be the highest record for the species in Baja California. Stebbins (1954:303) reported *A. pulchra* from 1,950 m in the Giant Forest, Sequoia National Park in California. Its preference for moist, fine-textured soils, as reported by Miller (1944), probably limits *A. pulchra* to arroyo bottoms and coastal localities within the Mártir Region; its upward distribution in the Sierra is probably restricted by the steep, granitic west scarp.

Bury (1983) reported *Anniella pulchra* from an arroyo on the West Scarp of the Sierra Juárez, 60 km east southeast of Ensenada. Klauber (1932) recorded *A. pulchra* at Cañón San Salado, at the base of the East Scarp of the Sierra Juárez. Bury (1983) maintained that this locality is probably Arroyo Salado, 19 km south of San Vicente near the Pacific coast; he indicated that a second record from the Gulf Slope near San Felipe is also probably invalid.

SERPENTES

Leptotyphlopidae

Leptotyphlops humilis cahuilae Klauber, 1931b,
Desert Worm Snake

Leptotyphlops humilis humilis
(Baird and Girard, 1853),
Western Worm Snake

Klauber (1940) reported two subspecies of *Leptotyphlops humilis* in northern Baja California: *L. h. humilis* occurs on the Pacific Slope from San Diego County, California, south into the Central Desert Region, and *L. h. cahuilae* occurs along the Gulf Slope from California into central Baja California. Klauber also noted a record of *L. h. cahuilae* from the Vizcaino Desert.

I collected two specimens of *Leptotyphlops humilis* on the lower Pacific Slope of the Mártir

Region: one was taken at 1950 hr, as it moved rapidly across a dirt road at 1,100 m in open, sandy, coastal sage, 6.2 km west of station 28 (MVZ 140861); the other was found at station 27 (MVZ 140862), crushed in a cow track. Both specimens agreed in dorsal pigmentation and in number of pigmented scale rows with the description of *L. h. humilis* (Klauber 1940). However, the specimen from station 27 had a dorsal scale count (285) exceeding that established for *L. h. humilis* (range 257–283), and in the range for *L. h. cahuilae* (280–305). This suggests a zone of intergradation on the Pacific Slope of the Mártir Region.

Previously unpublished records of *Leptotyphlops humilis humilis* on the Pacific Slope include 25 km east of San Telmo (CAS 123717) and 8.3 km south of Socorro Ranch (SDNHM 19231), San Telmo (SDNHM 42746).

Leptotyphlops humilis cahuilae was first reported from the south Colorado Desert at Punta San Felipe (Murray 1955); additional records are known from 58.5 km north of San Felipe (SDNHM 44262–63) and 8.3 km north of San Felipe (CAS 136368–69). There are three records for this subspecies from Bahía de Los Angeles, at the south end of the Colorado Desert (CAS 103465, LACM 2167, and SDNHM 19998). Klauber (1940) reported this subspecies as far south as the Vizcaino Desert.

All records for the races of *Leptotyphlops humilis* from the Mártir Region are from areas of scrub vegetation.

Boidae

Lichanura trivirgata roseofusca Cope, 1868,
Coastal Rosy Boa

Three forms of the Rosy Boa are now recognized on peninsular Baja California. Klauber (1933), Lowe (1964), and Stebbins (1966) indicated that there are three subspecies (*Lichanura trivirgata trivirgata*, *L. t. gracia*, and *L. t. roseofusca*). Klauber (1931a) implied that *L. t. gracia* was intermediate between *L. t. trivirgata* and *L. t. roseofusca* on the basis of scale counts and color description. Gorman (1965) found no evidence of intergradation between *L. t. trivirgata* and *L. t. gracia*, and recognized two species: *L. trivirgata* and *L. roseofusca*.

Bostic (1971) reported two specimens from the Central Desert of Baja California that were sim-

ilar to Klauber's (1931a) description of *Lichanura trivirgata gracia*, but with dorsal and ventral scale counts matching *L. t. trivirgata*. One of these specimens was collected 167 km north of San Ignacio in the Vizcaíno Desert, previously the northernmost locality known for *L. t. trivirgata* in Baja California (Gorman 1965). This form is known from the Cape Region of Baja California and the west coast of México.

In the Mártir Region, the Rosy Boa is known from the lower Pacific Slope at numerous localities in the Western Foothills and on the San Quintín Plain, all corresponding to areas of coastal sage and Central Desert scrub. Specimens from this area match the description for *Lichanura trivirgata roseofusca*, which ranges north into California along the Pacific coast. Gorman (1965) ascribed a single specimen from the South Colorado Desert, 25 km south of San Felipe, to *L. roseofusca*. Welsh and Bury (1984) reported a specimen matching Klauber's (1931a) description for *L. t. gracia* from 56 km northwest of San Felipe in the Sierra San Felipe of the South Colorado Desert. *L. t. gracia* occurs in the high deserts of California and Arizona between the coastal California range of *L. t. roseofusca*, and the extreme southern Arizona and Sonora range of *L. t. trivirgata*. The northern Mojave Desert range of *L. t. gracia* is about 335 km away from the Central Desert and South Colorado Desert regions of Baja California where Bostic (1971) and Welsh and Bury (1984) collected *L. t. gracia*.

In view of this great distance, and the lack of low desert records for the species north of Baja California, it seems highly unlikely that a contiguous population of *Lichanura trivirgata gracia* exists across this area. The disjunct distribution of *L. t. gracia* between populations of *L. t. roseofusca* and *L. t. trivirgata* prompted my suggestion (Welsh 1976a) that *L. t. gracia* is a recurrent intermediate form, a thesis more recently entertained by Yingling (1982).

Colubridae

Arizona elegans eburnata Klauber, 1946b,
Desert Glossy Snake

Arizona elegans occidentalis Blanchard, 1924,
Western Glossy Snake

Arizona elegans pacata Klauber, 1946b,
Peninsula Glossy Snake

Klauber (1946b) reported *Arizona elegans occidentalis* at numerous localities along the Pacific Slope from the Mártir Region north into California. It has been reported as far south as El Rosario on the Pacific coast (SDNHM 44155). Seifert (1980) reported two specimens from the Central Desert south of Laguna Chapala.

A second subspecies, *Arizona elegans pacata*, is known from the Central Desert Region. Records are known from near Santo Domingo (Klauber 1946b), 43.4 km northwest of San Ignacio (Murray 1955), and 50 km west northwest of El Arco (Banta and Leviton 1963); more recently collected specimens are at CAS and MVZ (T. Papenfuss, pers. comm.).

Klauber (1946b) reported *Arizona elegans eburnata* in the Colorado Desert of California and Arizona, and implied its presence in north-eastern Baja California. In June 1974, I collected a juvenile male at 2030 hr, 3.2 km southeast of Rancho Rosarito (station 62; MVZ 140868). The site was a sandy arroyo with creosote bush scrub vegetation. The pattern and scutellation matched those described for *A. e. eburnata* (Klauber 1946b). This specimen, the first for the subspecies in Baja California, extended the range to 80 km southwest of San Felipe, and is also the first record of the desert glossy snake from the Pacific Slope. Welsh and Bury (1984) reported six more specimens of this race from Mártir Region localities northwest of San Felipe. All records of *A. elegans* from the Mártir Region occurred in areas of scrub vegetation.

Chilomeniscus cinctus Cope, 1861,
Banded Sand Snake

Chilomeniscus cinctus is known from six localities on the Pacific Slope of the Mártir Region: Arroyo Seco (SDNHM 48150–52), San Antonio River, northeast of Arroyo Seco (SDNHM 43378), 14 km east of San Telmo (SDNHM 41325), 20 km east of San Telmo (SDNHM 42737), and Valle de Trinidad (SDNHM 30371). The first five sites are in low-lying canyons that are immediately east and contiguous with the San Quintín Plain. These areas are dominated by Central Desert and coastal sage scrubs. Valle de Trinidad is at the northwest end of the Sierra and is dominated by creosote bush scrub that is contiguous through San Matías Pass into the Colorado Desert. The Valle de Trinidad record in-

dicates that *C. cinctus* is probably present in the sandy habitats of the South Colorado Desert.

R. Seib (pers. comm.) reported this species from two localities in the north Central Desert: Mission San Fernando 3.3 km west of El Progreso (MVZ 117449) and 5.5 km north of Santa Inés parador, Mexican Hwy 1 (MVZ 117303). Two other unpublished records exist for *Chilomeniscus cinctus* in this area: 16.7 km south of Cataviña (SDNHM 42054), and 50 km south of El Mármol (SDNHM 38663). Bostic (1971) reported a specimen from 0.8 km north of San Javier. Numerous additional records exist for the Central Desert southward throughout the peninsula (R. Seib, pers. comm.), including three unpublished records from San Ignacio (SDNHM 3828–30) in the Vizcaíno Desert.

Chionactis occipitalis annulata (Baird, 1859),
Colorado Desert Shovel-nosed Snake

The subspecies *Chionactis occipitalis annulata* is known from sandy alluvial soil in a limited coastal area north of San Felipe, within 3.2 km of the Gulf of California along Mexican Hwy 5 (Wake 1966a; Cross 1970). Welsh and Bury (1984) reported four more specimens from this area and two specimens from 11.2 km and 14.2 km west of the Gulf of California. This arenicolous snake is not known south of the Mártir Region; the discontinuity of suitable sandy habitat may account for its absence.

Coluber flagellum fuliginosus (Cope, 1895),
Baja California Coachwhip

Coluber flagellum piceus (Cope, 1875),
Red Coachwhip

Wilson (1973) indicated two subspecies of *Coluber flagellum* in the Mártir Region: *C. f. piceus*, ranging south through the Colorado Desert to the vicinity of Bahía de San Felipe, and *C. f. fuliginosus*, occurring at localities on the lower Pacific Slope, and south through the Central Desert. These areas contain scrub vegetation.

The dark phase of *C. f. fuliginosus* was observed twice during midmorning in open sandy coastal scrub at station 27 on the Pacific Slope. Both snakes were emerging from burrows. Another dark racer was observed above station 4 on the lower East Scarp but could not be identified to subspecies.

Wilson (1973) indicated a single record for

Coluber flagellum piceus in the South Colorado Desert, near San Felipe. Welsh and Bury (1984) reported seven records from inland localities north and west of San Felipe. These specimens were all red phase snakes.

Coluber lateralis lateralis (Hallowell, 1853),
California Striped Racer

Two records exist for *Coluber lateralis lateralis* on the East Scarp: Cañón el Cajón (Linsdale 1932), and Cañón del Diablo (SU 17298). On the Pacific Slope, this race is known from five localities: San Antonio Mine (Murray 1955), Valladares Creek (CAS 56881), Socorro (SDNHM 10524), and San José (SDNHM 5130 and 8856). I collected two specimens on the Pacific Slope: one dead on the road in rocky chaparral at 1,320 m near station 29 (MVZ 140863), and another at station 19 (MVZ 140864). An individual was observed at 1140 hr in a hollow oak trunk in oak woodland; this snake was feeding on a *Peromyscus* sp. Available records indicate a preference for chaparral and riparian habitats on the east and west scarps and on the lower Pacific Slope.

Diadophis punctatus similis Blanchard, 1923,
San Diego Ringneck Snake

Schmidt (1922) recorded *Diadophis punctatus similis* from San Matías Pass. This specimen was probably collected at a spring south of the Pass, and some 150 m higher, in pinyon-juniper woodland. This race is known from Rancho San José (SDNHM 36534), where it occurs in riparian habitat (Aida Meling, pers. comm.), and from an irrigated slope of Arroyo San Telmo, south of Colnett (R. Marlow, pers. comm.). These records, and habitat preferences of the species in other areas (Stebbins 1966), indicate it is probably restricted to the Pacific Slope of the Mártir Region, in riparian woodland corridors below 1,500 m elevation.

Elaphe rosaliae (Mocquard, 1899),
Baja California Rat Snake

Elaphe rosaliae, long known from San Bartolo and Santa Rosalía in Baja California Sur (Schmidt 1922; see Ottley and Jacobsen 1983 for additional localities), has been reported more recently from localities to the north. Hunsaker (1965) re-

ported two specimens at Cañón Guadalupe on the east scarp of the Sierra Juárez, and Stebbins (1985) reported a specimen from Mt. Spring, Imperial Co., California. These records indicate *E. rosaliae* ranges in the intervening area on the eastern slopes of the Peninsular Range through the Mártir Region (Stebbins 1985).

Hypsiglena torquata deserticola Tanner, 1946,
Desert Night Snake

Hypsiglena torquata klauberi Tanner, 1946,
San Diego Night Snake

Tanner (1966a) reviewed available material of *Hypsiglena torquata* and proposed that the Pacific Slope distribution for *H. t. klauberi* in Baja California was through the Mártir Region to the North Central Desert. Bostic (1971) reported a specimen of this race from near El Rosario. Tanner (1966a) suggested that *H. t. deserticola* occurs in northeastern Baja along the Gulf Slope. This was based on five specimens from the Central Desert Region that showed evidence of intergradation between *H. t. klauberi* and *H. t. deserticola*. Tanner also indicated that the species occurs near San Felipe. The above records and known habitat preferences of this species (Stebbins 1966) indicate that it probably inhabits all scrub and xeric woodland areas on both slopes of the Region.

Lampropeltis getulus californiae
(Blainville, 1835),
California Kingsnake

This snake is known from the East Scarp at Cañón El Cajón (Linsdale 1932). I observed a juvenile on the East Scarp at station 20. It was active in shade at 0840 hr on a rocky slope of pinyon-juniper woodland. This race is also known on the Gulf Slope at Bahía de San Luis Gonzaga (CAS 90227), an area of creosote bush scrub. Lower Pacific Slope records are relatively numerous, indicating that the snake occurs in coastal sage and Central Desert scrub south to El Rosario (SDNHM 1070, 41264). I observed two specimens on the lower Pacific Slope, at station 27; one was in coastal sage scrub, and the other under a cottonwood tree (*Populus* sp.) in a grassy field at the edge of riparian habitat. This snake has not been reported from the central South Colorado Desert or from the upper Sierran scarps.

Schmidt (1922) reported *Lampropeltis getulus yumensis* from Volcano Lake in the Colorado Desert of extreme northeastern Baja California. Two records from 11.6 km east of Cerro Prieto (32°25'N) are also in this area (MVZ 10761–62).

Lampropeltis zonata agalma
Van Denburgh and Slevin, 1923,
Baja California Mountain Kingsnake

I collected a single *Lampropeltis zonata agalma* active at 1635 hr in an area of rocky chaparral at 1,600 m, 1.7 km west of station 29 (MVZ 140871). This locality was about 10 km down slope from the nearest coniferous forest habitat. All other locality records for this snake in the Mártir Region (Zweifel 1952, 1974; SDNHM 46017; and R. Moran, pers. comm.) are from higher elevations, up to 2,800 m, in areas of coniferous forest.

Throughout its range, *Lampropeltis zonata* occurs sympatrically with the wide-ranging *L. getulus*, whose range circumscribes the areas occupied by *L. zonata* (Stebbins 1966). Storer and Usinger (1963) indicated that *L. getulus* is rare or absent in coniferous forests of the Sierra Nevada of California, habitat where *L. zonata* is found most commonly. *L. getulus* occurs up to 2,100 m (Stebbins 1966), but is uncommon in coniferous forest habitats, even where *L. zonata* is absent. Perhaps *L. getulus* is limited by an elevational factor such as temperature, and *L. zonata* replaces it in these higher, cooler areas. Out of coniferous forest habitats *L. zonata* is uncommon, but it does occur marginally in chaparral throughout its range (Zweifel 1952, 1974; this study).

Phyllorhynchus decurtatus perkinsi
Klauber, 1935,
Western Leafnose Snake

This snake is known in the Mártir Region only from the South Colorado Desert of the Gulf Slope; records exist from 21.8 km north of San Felipe (SDNHM 18917) and 1.6 km north of San Felipe (SDNHM 38108). Welsh and Bury (1984) reported four additional specimens from localities 50 km northwest of San Felipe. The subspecies *P. d. decurtatus* occurs from south of the Mártir Region through central Baja California and south into the Cape Region. Specimens are known from 16 km north of Rancho Cata-

viñá (LACM 20751), 16.2 km south of Punta Prieta (Bostic 1971), 16.7 km southeast of Mesquital (MVZ 50171) in the Central Desert, and from Bahía de Los Angeles (SU 21800) on the Gulf coast. R. Seib (pers. comm.) reported 14 additional records from the Central Desert southward.

Pituophis melanoleucus annectens

Baird and Girard, 1853,
San Diego Gopher Snake

Pituophis melanoleucus bimarís Klauber, 1946a,
Baja California Gopher Snake

Pituophis melanoleucus affinis Hallowell, 1852,
Sonoran Gopher Snake

Klauber (1946a) reported *Pituophis melanoleucus annectens* from numerous localities on the Pacific Slope of the Mártir Region up into coniferous forest, and north into California. Murray (1955) reported this form at 1,400 m in chaparral on the West Scarp. It is known along the coast at San Antonio del Mar (SDNHM 23800 and 32149), and Bostic (1971) reported this race in the Central Desert, 31.8 km southeast of El Rosario.

I collected three snakes that all correspond in pattern and color with *Pituophis melanoleucus annectens*. A snake was found crossing a road at 1730 hr, 15.2 km east of station 7 (MVZ 140869); a second individual was found on the road at 1400 hr, 4.8 km west of station 29 (destroyed in transit); and a third was found dead on the road in midafternoon at station 28 (MVZ 140870). The first locality was in an area of Central Desert/coastal sage scrub, and the other two sites were in areas of coastal sage scrub/chaparral ecotone.

The subspecies *Pituophis melanoleucus bimarís* occurs throughout the Central Desert (Klauber 1946a), whereas *P. m. affinis* is known from two localities in extreme northeastern Baja (Klauber 1946a). The latter form has not yet been reported in the desert east of the Sierra San Pedro Mártir, but Welsh and Bury (1984) reported a specimen from 9.1 km east of San Matías Pass that appears to be an intergrade between *P. m. affinis* and *P. m. annectens*.

Klauber (1946a) noted overlap in the ranges of *Pituophis melanoleucus annectens* and *P. m. bimarís* on the Pacific Slope through the Mártir Region, from El Rosario north to Alamo; he found

no evidence of intergradation in the specimens he examined from this area.

Rhinocheilus lecontei lecontei

Baird and Girard, 1853,
Western Longnose Snake

Klauber (1941) reported two records from extreme northeastern Baja California. Other records from this area include: 51.2 km east of Mexicali (LACM 36576), east of Mexicali (SDNHM 19884–85; LACM 20821), and Tajo Canyon (SDNHM 18875). Few records exist for the eastern Mártir Region; Medica (1975) reported one specimen from San Felipe, and Welsh and Bury (1984) reported a specimen from 50 km north and 12 km west of San Felipe. There are several records from the Pacific Slope, both north into California, and within the Mártir Region as follows: 3.2 km and 11.2 km south of Santo Tomás (LACM 59125, 102711), 8.3 km east of Cabo Colnett (SDNHM 34003), 3.3 km south of San Simón (SDNHM 42094), 3.3 km north of San Simón (SDNHM 42632), and 12.7 km north of Arroyo Seco (SDNHM 42543). These Pacific Slope localities are in areas of coastal sage and Central Desert scrub, whereas the records from the Gulf Slope correspond with areas of creosote bush scrub. Records from 1.7 km west of El Marmol (SDNHM 42439), 24.2 km south of Rancho Santa Inés (CAS 143725), and San Borja (SDNHM 42439) confirm this species in the Central Desert. Lockington (1880) reported this snake from the vicinity of Magdalena Bay in Baja California Sur, but Klauber (1941) doubted the validity of this record. The two recent specimens from the Central Desert Region, and a record from Cerralvo Island off the Cape Region (Soule and Sloan 1966), give renewed credence to Lockington's record. Medica (1975) stated that this species will probably be found to inhabit all of Baja California.

Salvadora hexalepis hexalepis (Cope, 1867),
Desert Patchnose Snake

Salvadora hexalepis klauberi Bogert, 1945,
Baja California Patchnose Snake

Salvadora hexalepis virgulata Bogert, 1939,
Coast Patchnose Snake

A specimen of *Salvadora hexalepis* was collected at 0707 hr crossing a sandy road in chap-

arral-coastal sage ecotone at 915 m, 5.8 km east of station 27 (MVZ 140865). A second individual was found at 0906 hr in chaparral at station 11 (MVZ 140866). Both specimens fit the description of *S. h. virgultea* (Bogert 1945). This subspecies is known from the Pacific Slope of northern Baja California, from California to the vicinity of El Rosario. Records in the Mártir Region indicate an affinity to areas of chaparral, coastal sage, and Central Desert scrub vegetations.

Bogert (1945) described *Salvadora hexalepis klauberi* from the Central Desert, and indicated a zone of intergradation between *S. h. klauberi* and *S. h. virgultea* in the vicinity of latitude 30°N (El Rosario). His speculation that *S. h. hexalepis* might range into northeastern Baja in the Colorado Desert was confirmed by a specimen from the Gulf Slope of the Mártir Region reported by Welsh and Bury (1984).

Sonora semiannulata Baird and Girard, 1853,
Western Ground Snake

Frost (1983) placed the two banded ground snakes of Baja California, *Sonora bancroftae* and *S. mosaueri*, in synonymy with the unbanded *S. semiannulata*; at that time he concluded that insufficient evidence existed to describe subspecies. Despite Frost's conclusion I think it important to bear in mind that the banded forms are superficially different from the unbanded *S. semiannulata*, and that their respective distributions are not inconsistent with other unique elements of the Baja California herpetofauna. Because of the possible zoogeographic implications of these populations I have chosen to treat the banded forms here as subspecies.

Stickel (1943) indicated that *S. semiannulata* occurred through the Colorado and Central Desert Regions of Baja California to Santa Rosalía; however Frost (1983) indicated a lack of records to confirm the species in the Colorado Desert east of the Sierra San Pedro Mártir.

Klauber (1943) described the banded form *Sonora bancroftae* from a single specimen collected in Arroyo San Telmo, 3.3 km east of San Jorge, a site on the lower Pacific Slope of the Mártir Region, in an area of Central Desert/coastal sage scrub ecotone. A second individual is known from Rancho Buena Vista (SDNHM 36527), 27 km further east and slightly higher in the same arroyo in coastal sage scrub.

Stickel (1938) described another banded form, *Sonora mosaueri*, from three specimens collected at Comondú in Baja California Sur. It has since been reported from the Vizcaíno Desert in the vicinity of Santa Rosalía (SDNHM 44468 and 46808), and in the Central Desert, 37 km south of El Rosario (SDNHM 46802). Stickel (1943) noted that *S. mosaueri* was closely related to, and might prove to be a subspecies of *S. semiannulata*. The distribution of the three forms of *Sonora* are in disparate, yet contiguous, areas of desert scrub vegetations.

Tantilla planiceps (Blainville, 1835),
California Blackhead Snake

Cole and Hardy (1981) recognized no subspecies of *Tantilla planiceps*. Tanner (1966b) reported five specimens from the Pacific Slope of Baja California, three from north of the Mártir Region, one from 6.4 km south of San Vicente in the Western Foothills, and one from the Central Desert. Bostic (1971) reported a specimen from the Central Desert, 39 km southeast of El Rosario. These localities indicate that *T. planiceps* occurs in coastal sage and Central Desert scrub vegetations within the Mártir Region. A single record exists from the Gulf Slope at Arroyo El Tajo on the east scarp of the Sierra Juárez (SDNHM 45001), indicating *T. planiceps* is probably also present on the Gulf Slope of the Mártir Region.

Thamnophis elegans hueyi
Van Denburgh and Slevin, 1923,
San Pedro Mártir Garter Snake

This endemic subspecies of *Thamnophis elegans* is found only on the Main Scarp of the Sierra San Pedro Mártir (Van Denburgh and Slevin 1923) and occurs in riparian meadow and nearby moist woodland habitats of the coniferous forest.

Elsewhere, *Thamnophis elegans* occurs at all elevations up to 3,000 m, and is associated with a variety of terrestrial and riparian habitats (Stebbins 1966). In the Mártir Region, *T. elegans* is found only in and around marshy meadows and slow streams above 1,820 m. *T. hammondi* is also present, but uncommon in these areas; it occurs more frequently in and around the fast-flowing streams in the steep riparian areas below the Main Scarp where *T. elegans* is absent. My observations of foraging of *Thamnophis* spp. in

the Mártir Region suggest that both species may be localized to riparian habitats because of the moisture requirements of their amphibian prey species. The usually eurytopic *T. elegans* may be further limited to marshy habitats of the main scarp by the presence of *T. hammondii*. Foraging strategies may be an important factor in segregating these two species in areas of sympatry such as the Lower Main Scarp. *T. hammondii* is noticeably more aquatic, and was seldom observed out of water. It was observed in pursuit of anuran larvae and *Hyla cadaverina*. *T. elegans* seemed to prefer moist or damp habitats but was not observed in the water. It was observed feeding on toads on marshy ground.

An adult female collected 22 June 1974 (station 24) (MVZ 140876) contained eight small ova. An adult female found under a log at 1916 hr had recently ingested an adult *Bufo boreas*. Specimens were collected at stations 12 (MVZ 140875), 25 (MVZ 140872), 37 (MVZ 140873), and 40 (MVZ 140874); observations were made at stations 24 and 39.

Thamnophis hammondii (Kennicott, 1860),
Two-striped Garter Snake

This snake occurs on the East Scarp and the Pacific Slope of the Region, frequenting only riparian habitat. It occurs to 2,120 m on the Lower Main Scarp in coniferous forest, on the East Scarp in creosote bush scrub and pinyon-juniper woodland, and on the Pacific Slope in arroyos dominated by chaparral and coastal sage scrub, ranging west to the San Quintín Plain. A juvenile was observed at station 65 in an irrigation ditch that flowed from an apparently permanent spring in Arroyo Eduardo, an area of Central Desert scrub. Records from El Rosario (SDNHM 41593; LACM 104069-71) are the southernmost for this species.

Thamnophis hammondii was observed underwater, along streamsides, on streamside rock faces, and up to 3.4 m above ground in riparian overstory (usually willow). I twice observed snakes in apparent pursuit of *Hyla cadaverina*. On three occasions, *T. hammondii* were observed underwater stalking and lunging at anuran larvae.

Specimens were collected at stations 17 (MVZ 140880), 37 (MVZ 140887, 147528), and 49 (MVZ 140878-79). Observations were made at stations 10, 16, 20, 21, 23, 27, 38, and 65.

Trimorphodon biscutatus vandenburghi
Klauber, 1924,
California Lyre Snake

An adult male, matching Gehlbach's (1971) description for *Trimorphodon biscutatus vandenburghi*, was found dead on a dirt road on the morning of 22 June 1973, at 1,520 m in rocky chaparral, 3.5 km west of station 29 (MVZ 140877). This subspecies is known in northwestern Baja California from six other specimens: 16 km north of Arroyo Seco on the San Quintín Plain (Murray 1955), 2.9 km north of El Rosario de Arriba (LACM 121552), 4.8 km east of La Rumerosa (SDNHM 121149), 2.2 km south of Cataviñá (CAS 146577), 27 km south of Santa Inés (MVZ 161561), and 32 km southeast of Punta Prieta (LACM 126261). Scott and McDiarmid (1984) showed a lack of records from the Gulf Slope of northeastern Baja California; Welsh and Bury (1984) reported the first specimen from 34 km east of San Matías Pass in the South Colorado Desert. Habitat preferences (Stebbins 1966) suggest the probable occurrence of this snake in pinyon-juniper, chaparral, and all scrub vegetations of the Mártir Region. The absence of contiguous rocky habitat may limit its distribution in parts of the Colorado Desert. Gehlbach (1971) indicated that *T. b. lyrophanes* of southern and central Baja California is known as far north as San Ignacio in the Vizcaíno Desert.

Vipiridae

Crotalus atrox atrox Baird and Girard, 1853,
Western Diamondback Rattlesnake

This snake ranges into the Colorado Desert of extreme northeastern Baja California (Schmidt 1922; Linsdale 1932), and has been reported from Central Baja California (Alvarez and Huerta 1974). It has yet to be found in the Mártir Region. Suitable habitat for this species occurs in the South Colorado Desert; its apparent absence may be due to limited collecting in this remote region.

Crotalus cerastes laterorepens Klauber, 1944,
Colorado Desert Sidewinder

Crotalus cerastes laterorepens is known from numerous localities in the South Colorado Desert from San Matías Pass to the vicinity of San Felipe (Linsdale 1932; Murray 1955; Welsh and

Bury 1984), south to San Francisquito on the Gulf coast (Klauber 1944). Residents of the Valle de Trinidad area informed me that it occurs at that Pacific Slope locality. All regional localities for this species are areas of creosote bush scrub. It has not been reported from the Pacific Slope south of the Mártir Region and the Gulf Slope south of San Francisquito. It may be excluded from these deserts by the presence of the closely related form *C. enyo*.

Crotalus enyo fuvus Lowe and Norris, 1954,
Dusky Baja California Rattlesnake

Crotalus enyo fuvus was described by Lowe and Norris (1954) from four specimens collected along the San Quintín Plain, north of El Rosario. Their proposed range for *C. e. fuvus*, based on vegetative and edaphic affinities, corresponds with Sonoran habitat of the Pacific coast of the Mártir Region (Short and Crossin 1967), herein considered as part of the Central Desert scrub vegetational association. Lowe and Norris's proposed range also corresponds closely to the San Quintín Plain. A record from 4.6 km north of Arroyo Seco (SDNHM 46196) is just north of this proposed range, in Central Desert scrub. Short and Crossin (1967) indicated that this habitat extends north to the vicinity of Rio San Antonio along the base of the foothills and as far as Punta Banda on the coast. Future work in the area may reveal that the northern limit of this snake corresponds closely with this habitat.

Crotalus enyo enyo is known in more arid habitats as far north as 17.2 km southeast of El Rosario (Bostic 1971), and from numerous southern localities of the Central Desert, Vizcaíno, and Cape Regions (Lowe and Norris 1954).

Crotalus mitchellii pyrrhus (Cope, 1867),
Southwestern Speckled Rattlesnake

Crotalus mitchellii pyrrhus occurs on the Gulf and Pacific slopes of the Mártir Region. I observed two snakes on the rocky East Scarp at stations 17 and 21 (MVZ 140884), in creosote bush scrub and pinyon-juniper, respectively. A third individual was observed on the lower West Scarp at station 28 in coastal sage-chaparral ecotone. Klauber (1936) indicated the occurrence of other records from the Mártir scarps, Western Foothills, and northward on both slopes into the southern U.S. The three snakes I observed were

active during midmorning among boulders. Literature records and my observations indicate that *C. m. pyrrhus* is primarily saxicolous, although some records exist for other than rocky habitat (Klauber 1972).

South of the Mártir Region on the Gulf Slope, *Crotalus mitchellii pyrrhus* is known from Bahía de Los Angeles (SDNHM 19713–14). Specimens from 4.8 km north of (LACM 20005) and 28.8 km south of (LACM 20006) Rancho Cataviña are apparently the first records of this species from the Pacific Slope of the Central Desert. The subspecies *C. m. mitchellii* occurs in the Vizcaíno Desert and south into the Cape Region of the Peninsula.

Crotalus ruber ruber Cope, 1892b,
Red Diamondback Rattlesnake

This subspecies occurs from San Diego County, California, south through the Mártir Region and the Central Desert (Klauber 1972). It has been reported from numerous localities on the lower Pacific Slope in the Western Foothills and on the San Quintín Plain (Klauber 1972). I found it in the sandy desert at the base of the East Scarp. Welsh and Bury (1984) reported it from a Gulf coast locality north of San Felipe.

I observed two specimens at the base of the East Scarp in creosote bush scrub. One was found active in late afternoon shade on an open sandy slope at station 54, the other at station 17, coiled in the midafternoon shade of an overhanging rock among talus. I collected one specimen at night on the Pacific Slope, beside a dirt road, 5 km north of El Burro (station 3) (MVZ 140885), in an area of chaparral-pinyon-juniper ecotone.

Crotalus viridis helleri Meek, 1905,
Southern Pacific Rattlesnake

I found nine records of *Crotalus viridis helleri* on the interior lower Pacific Slope of the Mártir Region, all corresponding with areas containing riparian woodland habitat: La Toya, Valladares Creek, and Rancho San José. Other records from the Mártir and Central Desert regions indicate that this species has an affinity for coastal habitats: San Antonio del Mar (CAS 57555); West of San Quintín Bay (SU 12141–42); Camalú Plains, 8.3 km north of Santo Domingo (SU 11574); Punta Camalú (CAS 40140); Playa Maria Bay (Klauber 1949); and 16.7 km south of

Jesús María (Bostic 1971). In the Sierra San Pedro Mártir, I found *C. v. helleri* up to 2,120 m on the Lower Main Scarp at stations 37 (MVZ 140822), 38 (MVZ 140883), and 39 (MVZ 147529), in coniferous forest and in conifer-chaparral ecotone. This snake was most often encountered in riparian edge habitat in these areas. I also found a specimen in open chaparral at 1,300 m. It was coiled in sand on a road at 2008 hr. *C. v. helleri* has not been reported from the Gulf Slope of the Mártir Region.

This species frequents riparian, coastal, and upland habitats but is apparently absent from inland scrub areas of the Mártir and Central Desert regions. However, two records are known from arid situations in the Central Desert: 33.4 km northwest of Bahía de Los Angeles (Klauber 1949), and 33.4 km southeast of Mezquital (Murray 1955). Specimens from the Central Desert are described by Murray (1955) and Bostic (1971) as light in color. Specimens I found in the Mártir Region were dark, almost black.

Jones (1981) and Ottley and Hunt (1981) reported two records of *Crotalus viridis helleri* from Baja California del Sur; these specimens represent the southernmost records for the species.

ZOOGEOGRAPHIC ANALYSES

I used both a numerical analysis and a heuristic comparison of distributions (based on locality records listed in Species Accounts) across the matrix of ecogeographic formations (Fig. 14) to determine distributional patterns within the Region. Regional patterns were then extrapolated beyond the Region to include the entire distribution of each species in order to test for overall geographic congruency between species linked by a common ecogeographic pattern within the Region (analysis of tracks). Evidence of such overall distributional congruency was considered indicative of a common evolutionary history among linked species.

Numerical Analysis

Cheetham and Hazel (1969) reviewed and discussed the use of numerical methods (Faunal Resemblance Factors or FRFs) in biogeography, noting the inherent advantages, disadvantages, and assumptions associated with binary coefficients. They listed some 22 possible formulas for expressing the relationship of the number of taxa

in common between paired geographic units to the total number of taxa present. In order to ameliorate the disadvantages inherent with any particular FRF, I employed three different FRFs that tend to complement one another by emphasizing different aspects of faunal assemblages. An FRF that emphasizes similarities can indicate historical affinities and evolutionary relationships between geographic areas, whereas an FRF that emphasizes differences can test for sampling error and the effects of faunas of unequal size, situations minimized by similarity coefficients. In addition to using a coefficient of similarity and a coefficient of difference, I used a third coefficient, one that emphasizes ecological relationships between geographic units—a community coefficient (Jaccard 1902). Subspecific differences were ignored for this analysis; distributions were determined by species.

All available records (see Species Accounts) were plotted on a schematic, southwest to northeast, regional transect in the vicinity of latitude 31°N (all localities used are between 30°30'N and 31°30'N latitude). The ecotones between regional ecogeographic formations (Fig. 14) were used to delineate the units along the transect used for numerical comparison. A species was considered to occur within an ecogeographic formation only if it ranged across the ecotone; marginal species, those found only to occur in the ecotone and not in a particular ecogeographic formation, were not included. The fauna of each formation was compared with those of all other formations using the following three FRFs: Savage's (1960) Coefficient of Difference ($CD = 1 - C/N_2 \times 100$); Simpson's (1960) Similarity Coefficient ($SC = C/N_1 \times 100$), and Jaccard's (1902: *in* Morafka 1977) Community Coefficient ($CC = [(C/N_1 + N_2 - C) \times 100]$), where C = the number of species in common, N_1 = the number of species in the area with the fewest species, and N_2 = the number of species in the area with the most species.

Faunal resemblance factors are descriptive rather than statistical indices (Cheetham and Hazel 1969) and thus do not have levels of significance. I established a "level of significance" for each coefficient on the basis of usage by previous workers, and the relative correlation of the different coefficient values derived from the comparison of geographic units where N_1 approaches or equals N_2 . My primary emphasis, when eval-

uating FRF values, was to weigh all three values for each pair of geographic units, treating all units relative to one another, and to look for obvious clusters occurring in ranked coefficient values. Savage (1960) arbitrarily selected $CD = 50\%$ or greater as indicative of a unique faunal grouping and I follow his usage as a basis. Employing the 50% level of significance with Jaccard's CC and Simpson's SC indicated to me that they are more sensitive and less sensitive, respectively, than the CD for distinguishing unique faunal groupings. I have therefore partially weighted these coefficients. Those ecogeographic formation pairs with at least two of three coefficients meeting the following criteria: $CD < 50\%$, $CC \geq 40\%$, and $SC \geq 60\%$, were considered to be related at a significant level.

Thirteen pairs met my criteria for significant relatedness (Table 4). The relationships between these 13 pairs are depicted phenographically (Fig. 15a-c). Subsequent pairwise analyses between ecogeographic formations using both average linkage (UPGMA) and single linkage (nearest neighbor) methods (SAS 1985) yielded results nearly identical to those depicted in Figure 15a-c.

Results of the numerical comparison indicate the presence of four distinct herpetofaunal areas within the Mártir Region, each showing some degree of overlap with one or more of the adjacent areas (Fig. 15a-c). These areas are:

(1) The Upper Main Scarp and the Lower Main Scarp—these two formations support the same montane herpetofauna ($SC = 100\%$) with numerous species dropping out with increasing elevation ($CD = 60\%$). The unequal fauna sizes between these two formations (7 vs. 20) account for the high SC and low CC values ($CC = 40\%$).

(2) The Lower Main Scarp, West Scarp, and the Western Arroyos—these three formations support a fauna that apparently shares some ecological characteristics and possibly a convergent history with that of (1) above, but differ in their adaptation to the warmer and drier habitats of lower elevations, extending into some relatively extreme xeric areas where these species occur along the riparian corridors of the Western Arroyos, and similar habitats of the East Scarp.

(3) East Scarp and West Scarp—the high SC and CC and the low CD values between these formations indicate strong faunal affinities between these two rocky xeric woodland areas.

However, each of these two formations demonstrates only slightly less significant, differing affinities, with proximal formations; a situation that initially seems somewhat contrary and confusing. The East Scarp shows close faunal links with the Colorado Desert and the Western Foothills, while the West Scarp shows close affinities with the Western Arroyos and the Western Foothills (the FRF comparisons of the West Scarp and the Western Foothills are not depicted phenographically in Fig. 5a-c because they fell just below my levels of significance: $CD = 49\%$, $SC = 55\%$, and $CC = 36\%$). I interpret these data to mean that two distinct overlapping faunas are present on the East and West scarps, each continuing with slightly differing distributions onto adjacent formations.

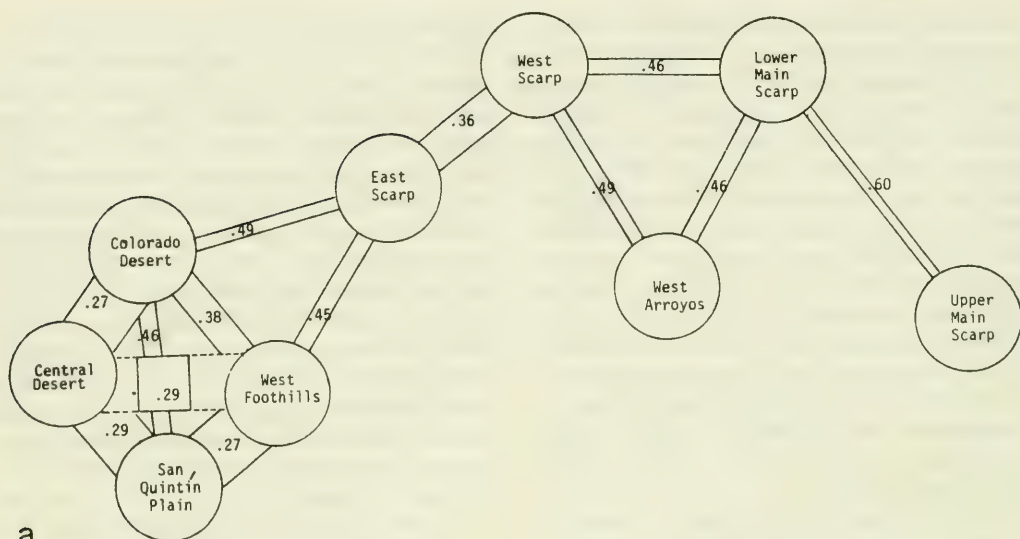
(4) The Colorado Desert, North Central Desert, San Quintín Plain, and the Western Foothills—all coefficient values between these four relatively open, scrub desert formations indicate strong faunal ties.

Further analysis of these numerical comparisons follows in conjunction with the results of the heuristic analysis below.

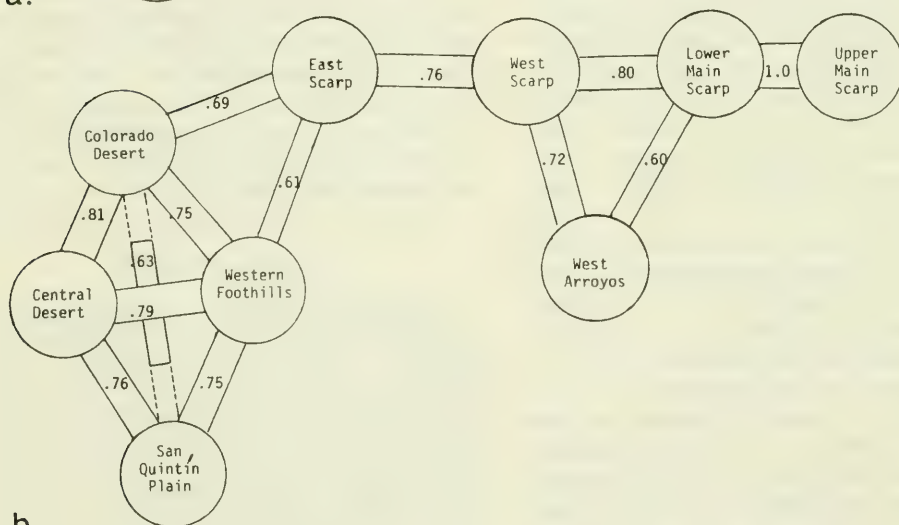
Heuristic Analysis

The heuristic analysis of distributions of regional species consisted of two parts: (1) a comparison of ecogeographic distributions along a schematic, southwest to northeast, regional transect between latitudes $30^{\circ}30'N$ and $31^{\circ}30'N$ (results depicted in Table 5); (2) a comparison of overall regional distributions established by plotting available literature and field records (Species Accounts) on maps based on Figures 3, 4, and 5 (results illustrated in Fig. 16). A species that occurred at two or more localities within a contiguous vegetation or physiographic area was assumed to occur throughout the contiguous habitat where suitable microhabitat existed, but not above or below the highest or lowest elevation records. I included locality records from the Sierra Juárez Region to the north and the Central Desert Region to the south to discern distributional trends over a wider area.

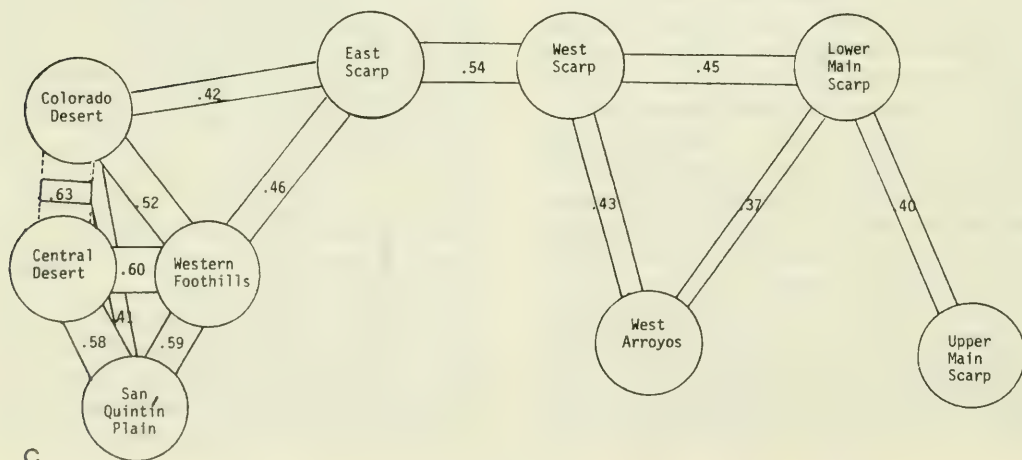
Three distinct patterns were apparent from the transect analysis (Table 5): (1) the High Sierran Fauna (I), with distributions corresponding closely to those of the Upper and Lower Main Scarp formations, areas linked by numerical



a.



b.



c.

TABLE 4. COMPARISON OF REGIONAL HERPETOFAUNAS BY ECOGEOGRAPHIC FORMATION (FIG. 14) USING THREE FAUNAL COEFFICIENT FACTORS.¹ Number of species present in parentheses. C = number of species in common. Formation pairs with two of three coefficients as follows are considered to be related at a significant level: CD < 50%, SC ≥ 60%, CC ≥ 40%.

East Scarp (26)	C	18							
	CD	49%							
	SC	69%							
	CC	41%							
Upper Main Scarp (8)	C	0	0						
	CD	100%	100%						
	SC	0%	0%						
	CC	0%	0%						
Lower Main Scarp (20)	C	3	9	8					
	CD	92%	66%	60%					
	SC	15%	45%	100%					
	CC	7%	24%	40%					
West Scarp (31)	C	12	20	6	16				
	CD	66%	36%	81%	49%				
	SC	38%	76%	75%	80%				
	CC	22%	54%	18%	45%				
West Foothills (29)	C	22	16	1	5	16			
	CD	38%	45%	97%	83%	49%			
	SC	75%	61%	12%	25%	55%			
	CC	52%	46%	3%	11%	36%			
West Arroyos (22)	C	2	9	4	12	16	5		
	CD	94%	66%	82%	46%	49%	83%		
	SC	9%	40%	50%	60%	72%	22%		
	CC	4%	23%	15%	37%	43%	10%		
San Quintin Plain (30)	C	19	13	2	5	15	22	8	
	CD	46%	57%	94%	84%	52%	27%	74%	
	SC	63%	50%	25%	25%	50%	75%	36%	
	CC	41%	30%	6%	11%	32%	59%	18%	
Central Desert (32)	C	26	15	2	6	14	23	6	23
	CD	27%	54%	94%	82%	57%	29%	82%	29%
	SC	81%	57%	25%	30%	45%	79%	27%	76%
	CC	63%	34%	5%	13%	28%	60%	12%	58%
		Colo. Desert	East Scarp	Upper Main Scarp	Lower Main Scarp	West Scarp	West Foot- hills	West Ar- royos	San Quintin Plain
		(35)	(26)	(8)	(20)	(31)	(29)	(22)	(30)

¹ CD = Coefficient of Difference ($CD = 1 - C/N_2 \times 100$) (Savage 1960); SC = Similarity Coefficient ($SC = C/N_1 \times 100$) (Simpson 1960); CC = Community Coefficient [$CC = (C/N_1 + N_2 - C) \times 100$] (Jaccard 1902, in Morafka 1977). N_1 = number of species in the area having the fewest species, N_2 = the number of species in the area with the most species.

comparison above, and indicating a montane fauna; (2) the Californian Fauna (II) with distributions corresponding closely to those of the second faunal area indicated numerically above, and encompassing primarily the Lower Main and West scarps and the Western Arroyos; and (3) the Colorado Desert Fauna (III). The endemic Colorado Desert Fauna is apparently too small, relative to the total number of xerophilic species present within the South Colorado Desert formation, to have been detected by the FRF analysis. The considerable overlap in ecogeographic

FIGURE 15. Relationships between herpetofaunas of the ecogeographic formations (Fig. 14) based on (a) Coefficients of Difference (CD) (Savage 1960), (b) Coefficients of Similarity (SC) (Simpson 1960), and (c) Community Coefficients (CC) (Jaccard 1902, in Morafka 1977). Width of bars is directly proportional to degree of relationship, length of solid bars is inversely proportional to degree of relationship. Formation pairs with CD > 0.50 not included (except the Upper Main Scarp for which the smallest value is included). Formation pairs with SC < 0.60 not included. Formation pairs with CC < 0.37 not included. See Table 4 for all pairwise values.

SPECIES

EOGEOGRAPHIC FORMATION¹

	N	S	W	W	W	L	U	E	C
	C	Q	A	F	S	M	M	S	D
	D	P				S	S	(P-J,	
	(CDS) ²	(CDS)	(RW)	(CSS)	(Chp)	(Con)	(Con)	CBS)	(CBS)
Regional Herpetofaunas									
IV. Peninsular Range Fauna									
A. Pacific Slope Forms:									
Anniella geronimensis**		X X							
Cnemidophorus hyperythrus	X				X				
Cnemidophorus labialis**	X	X							
Phrynosoma coronatum	X		X	X		X ?			
Crotalus enyo	X	X							
Sonora s. bancroftae		? X	X	X ?					
B. Rocky Scarps Forms:									
Crotaphytus insularis	X				X			?--X--?	
Petrosaurus mearnsi								X X	
Phyllodactylus nocticolus		X						X X	
Sauromalus obesus								X X	
Sceloporus orcutti	X	X	X			X		X X	
Urosaurus microscutatus			X	X	X			X X	
Xantusia henshawi**				X X		X		X X	
Crotalus mitchellii	?			X X	X--?			?--X X	
C. Flatland Desert Forms:									
Callisaurus draconoides		X			X			X X	
Dipsosaurus dorsalis								X X	
Chilomeniscus cinctus	X	X	X	X X				X--?	
Crotalus ruber	X		X	X		X		X X--?	
Lichanura trivirgata	?--X		X	X X--?				?-X X	
Phyllorhynchus decurtatus								X X	
V. North American Ubiquitous									
Scrubland Fauna									
Bufo punctatus	X					X		X X	
Schaphiopopus couchii								?--X--?	
Cnemidophorus tigris	X		X	X		X		X X	
Coleonyx variegatus	X X-----?			X X				X X	
Gambelia wislizenii	X		X	X X				X X	
Sceloporus magister	X		X	X		X		?--X X	
Uta stansburiana	X		X	X		X		?-X X	
Arizona elegans	X		X	?--X--?				X X	
Hypsigenia torquata	X		X	X		X-----?		?--X X	
Lampropeltis getulus	?--X					X--?		?--X X	
Leptotyphlops humilis	?--X--X--?--X--?							?--X	
Coluber flagellum	X		X	X	X			?--X X	
Pituophis melanoleucus	X					X		?--X--?	
Rhinocheilus lecontei	X		X	--?--				?--X-X	
Salvadora hexalepis	X		X	X		X--?		?--X X	
Sonora s. semiannulata	?--X--?							?--X--?	
Tantilla planiceps	X-----?			?--X				?--X--?	
Trimorphodon biscutatus	?--X--X					X--?		?--X--?	

{-----edotones-----}

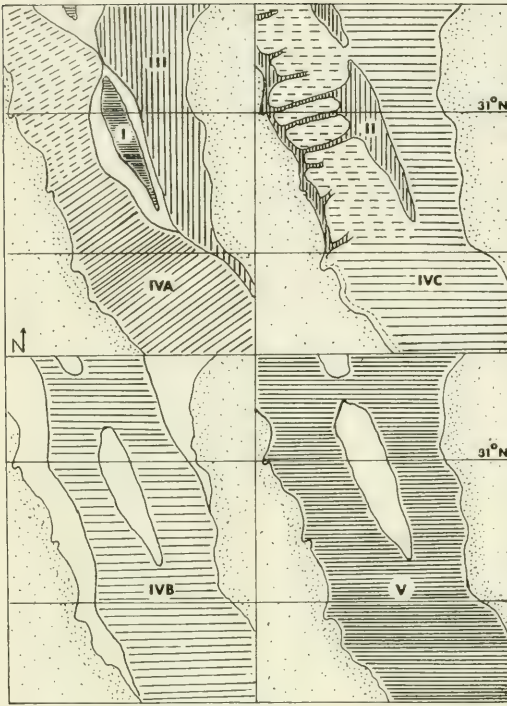


FIGURE 16. Distribution patterns of the herpetofauna of the Sierra San Pedro Mártir Region, Baja California Norte, México. Numerals refer to Table 5. In some cases member-species occur within, but not across the entire pattern range depicted; see Table 5 for exact regional distributions of individual species. Broken lines indicate fewer species of grouping indicated occur northward.

three derived above and numerically. The remaining species represent two relatively distinct groupings that occur throughout the xeric scrubland formations on both the Pacific and Gulf slopes (Fig. 16, pattern V), or only within some of the scrubland formations on one or the other, or both, slopes (Fig. 16, patterns IVa, IVb, IVc). Several species subsequently assigned to pattern IVc (Fig. 16) (*Callisaurus draconoides*, *Chilomeniscus cinctus*, *Crotalus ruber*, and *Lichanura trivirgata*) and pattern IVb (Fig. 16) (*Crotalus mitchellii*) had regional distributions that were indistinguishable from members of pattern V (Fig. 16) at this stage of analysis. Final assignment of these species, and those assigned to pattern V, was not possible until overall distribution patterns were compared (see Analysis of Tracks below).

The remaining three species assemblages (Fig. 16, patterns IVa, IVb, and IVc) are centered primarily along the East or West scarps or both, and

the Western Foothills, corresponding with the third faunal area derived numerically above (Fig. 15). This third FRF-derived faunal area is the least clearly defined probably due to the complex overlapping ecogeographic variations apparent among the several groups of species within this faunal area and their overlap with many of the species of pattern V. Pattern V (Table 5) corresponds closely with the fourth faunal area derived by the FRF analysis and covering the four scrubland desert formations (Fig. 15). Most species of pattern IVa (Fig. 16; Table 5) occur only on the Pacific Slope of northern or central Baja California. *Sonora semiannulata bancroftae* and *Anniella geronimensis* are endemic to the Mártir Region; *Crotalus enyo* and *Cnemidophorus labialis* have their northern limits slightly north of the Mártir Region. The remaining two members of pattern IVa (*Phrynosoma coronatum* and *Cnemidophorus hyperythrus*) range north across the U.S. border on the Pacific Slope. All of these species avoid rocky substrates, preferring sandy soils. Members of pattern IVc also show preference for sandy, fine-textured substrates, but demonstrate wider regional and overall distributions than members of pattern IVa, occurring throughout the xeric and subxeric scrub habitats on both the Pacific and Gulf slopes and ranging extensively beyond the Mártir Region (Fig. 16; Table 5). Pattern IVb species (Fig. 16; Table 5) are saxicolous species associated with the Peninsular Range scarps and bordering rocky scrubland habitats. Three of these species (*Petrosaurus mearnsi*, *Phyllodactylus nocticolus*, and *Sauromalus obesus*) occur only along the Gulf Slope north of 30°N latitude. The remaining pattern IVb members occur on both slopes of the Peninsular Range regionally and northward, except *Crotaphytus insularis*, which is absent from the Pacific Slope north of 32°N latitude. *Xantusia henshawi* is absent south of 30°N latitude.

Analysis of Tracks

Lastly, I conducted an analysis of the entire distribution of each taxon in Baja California using the Species Accounts and the following literature: Van Denburgh (1922), Schmidt (1922), Savage (1960, 1967), Soule and Sloan (1966), Stebbins (1966, 1985), Bostic (1971), Loomis et al. (1974), Conant (1975), Murphy (1983a), and Murphy and Ottley (1983, 1984). This last stage of the analysis sought to discern the generalized

tracks of the Baja California herpetofauna by comparing the geographic distributions of consanguineous forms (monophyletic lineages), seeking spatial congruency among unrelated taxa, the panbiogeographic method of Croizat (1964; see also Craw [1983] and Craw and Weston [1984]). Distributions were examined and compared for each lineage at the subspecific, specific, and generic levels. In each case of a proposed generalized track, the number of individual tracks indicative of the described generalized track exceeded the minimum three taxon/area statements (three individual tracks) considered as essential to support a hypothesis of a generalized track or pattern (Craw 1983).

I found evidence of at least five generalized tracks among the herpetofauna of the Sierra San Pedro Mártir Region: a Northwest Pacific Track, a Madrean Track, a Colorado Desert Track, a Peninsular Range Track, and a North American Desert and Plains Track.

The Pacific Northwest Track (Fig. 17)

The 20-plus species on this track are found along the western Pacific rim from Baja California north through California, Oregon, Washington, and into Canada, with a few forms occurring north to Alaska. Many species of this track have allopatric congeners in the northeastern United States. This track is characterized by endemic salamanders, most of which occur north of 35°N latitude in California; only the genera *Ensatina* and *Aneides* occur in Baja California. In southern California and Baja California, members of the Pacific Northwest Track (Table 6) occur as disjunct populations and are often isolated on mountain ranges. *Clemmys marmorata* is the only reptile of the Mártir Region that I believe is a member of this track. The anurans *Bufo boreas* and *Rana aurora* are included on this track, but their taxonomic and distributional patterns do not match the pattern as well as the other amphibians indicated. This may be due to their euryecious nature, and they may in fact have a common zoogeographic history with other track members. They may also represent another, more recent overlapping track, as they appear to be relatively young forms in North America that may have relatively recently diffused (Pielou 1979) south across cool temperate regions (Savage 1960). The Mártir faunal elements of the Pacific Northwest Track are mem-

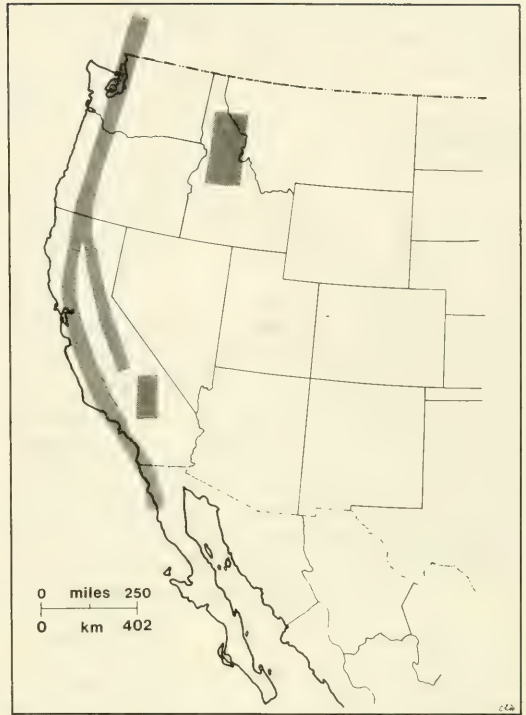


FIGURE 17. Generalized tracks of the herpetofauna of the Baja California Region: Pacific Northwest Track.

bers of either the High Sierran or Californian faunas (Table 5; Fig. 16, I and II) and have their southern terminus in the Mártir Region.

The Madrean Track (Fig. 18)

The Madrean Track lineages exhibit a complex pattern of distribution across southwestern North America often involving two or more disjunct forms, for each lineage, within Baja California and additional disjunct, closely related forms, to the north and east in California and Arizona, with many lineages ranging into southwestern New Mexico and south into the Sierra Occidental of Mexico (not all member lineages presently occur across the full range of the track). These forms avoid lowland xeric habitats for the most part, or if they occur in such areas, they have adapted to microhabitats, and temporal activity patterns that ameliorate against the extremes of low moisture and high temperature (e.g., *Scaphiopus*, *Xantusia* spp.).

Within Baja California many of these forms occur in disjunct populations, with some occur-

TABLE 6. RESIDENT TAXA OF THE GENERALIZED TRACKS OF THE HERPETOFAUNA OF THE BAJA CALIFORNIA REGION. Includes only those track members that occur within the Baja California Region. () refer to Figures 17–21.

Pacific Northwest Track (17)		
<i>Aneides lugubris</i>		<i>Rana aurora</i>
<i>Ensatina eschscholtzii</i>		<i>Clemmys marmorata</i>
<i>Bufo boreas</i>		
Madrean Track (18)		
<i>Batrachoseps pacificus major</i>	<i>Eumeces gilberti</i>	<i>Diadophis punctatus</i>
<i>B. pacificus</i> spp.	<i>E. skiltonianus</i> complex	<i>Coluber lateralis</i> complex
<i>Scaphiopus hammondii</i>	<i>E. skiltonianus</i>	<i>C. aurigulus</i>
<i>Bufo microscaphus</i>	<i>E. lagunensis</i>	<i>C. barbouri</i>
<i>Hyla cadaverina</i>	<i>Cnemidophorus labialis</i>	<i>C. lateralis</i>
<i>H. regilla</i>	<i>Elgaria</i> complex	<i>Lampropeltis zonata</i>
<i>Rana boylei</i>	<i>E. cedrosensis</i>	<i>Thamnophis hammondi</i> complex
<i>Sceloporus graciosus</i>	<i>E. multicarinata</i>	<i>T. hammondi</i>
<i>S. occidentalis</i>	<i>E. paucicarinata</i>	<i>T. digueti</i>
<i>Xantusia vigilis</i> (2 spp.)	<i>Anniella pulchra</i>	<i>T. elegans</i>
<i>X. henshawi</i>	<i>A. geronimensis</i>	<i>Crotalus viridis</i>
Colorado Desert Track (19)		
<i>Phrynosoma mcallii</i>		<i>Urosaurus graciosus</i>
<i>P. platyrhinos</i>		<i>Chionactis occipitalis</i>
<i>Uma notata</i>		<i>Crotalus cerastes</i>
Peninsular Range Track (20)		
<i>Chrysemys scripta</i>	<i>Sator</i> complex	<i>Cnemidophorus deppei</i> complex
<i>Bipes biporus</i>	<i>S. angustus</i>	<i>C. ceralbensis</i>
<i>Coleonyx switaki</i>	<i>S. grandaevus</i>	<i>C. hyperythrus</i> (3 spp.)
<i>Phyllodactylus angelensis</i>	<i>Sauromalus</i> complex	<i>Lichanura trivirgata</i> (3 spp.)
<i>P. apricus</i>	<i>S. ater</i> (2 spp.)	<i>Chilomeniscus</i> complex
<i>P. bugastrolepis</i>	<i>S. australis</i>	<i>C. cinctus</i>
<i>P. homolepidurus nolascoensis</i>	<i>S. hispidus</i>	<i>C. punctissimus</i>
<i>P. nocticolus</i> (9 spp.)	<i>S. klauberi</i>	<i>C. savagei</i>
<i>P. partidus</i>	<i>S. obesus</i>	<i>C. stramineus</i> (2 spp.)
<i>P. santacruzensis</i>	<i>S. slevini</i>	<i>Elaphe rosaliae</i>
<i>P. tinklei</i>	<i>S. varius</i>	<i>Eridiphas slevini</i> (2 spp.)
<i>P. unctus</i> (3 spp.)	<i>Sceloporus magister</i> complex	<i>Nerodia valida</i>
<i>P. xanti</i>	<i>S. m. lineatulus</i>	<i>Phyllorhynchus decurtatus</i> (3 spp.)
<i>Callisaurus draconoides</i> (6 spp.)	<i>S. m. monseratensis</i>	<i>Sonora semiannulata bancroftae</i>
<i>Crotaphytus insularis</i> (2 spp.)	<i>S. m. rufidorsum</i>	<i>S. s. mosaueri</i>
<i>Ctenosaura hemilopha</i>	<i>S. m. zosteromus</i>	<i>Tantilla planiceps</i>
<i>Petrosaurus</i> complex	<i>Sceloporus orcutti</i> complex	<i>Crotalus atrox</i> complex
<i>P. mearnsi</i>	<i>S. hunsakeri</i>	<i>C. catalinensis</i>
<i>P. repens</i>	<i>S. licki</i>	<i>C. exsul</i>
<i>P. thalassimus</i>	<i>S. orcutti</i>	<i>C. ruber</i> (2 spp.)
<i>Phrynosoma coronatum</i> complex	<i>Urosaurus</i> complex	<i>C. tortugensis</i>
<i>P. cerroense</i>	<i>U. lahtelai</i>	<i>C. emyo</i> (3 spp.)
<i>P. coronatum</i> (3 spp.)	<i>U. microscutatus</i>	<i>C. mitchellii</i> (4 spp.)
	<i>U. nigricaudus</i>	
North American Desert and Plains Track (21):		
Group A: old vicariated lineages		
<i>Bufo punctatus</i>		<i>Leptotyphlops humilis</i> (5 spp.)
<i>Scaphiopus couchii</i>		<i>Hypsiglena torquata</i> (7 spp.)
<i>Coleonyx variegatus</i> (6 spp.)		<i>Lampropeltis getulus</i> complex
<i>Uta</i> complex		<i>L. catalinensis</i>
<i>U. antigua</i>		<i>L. getulus</i> (3 spp.)
<i>U. nolascoensis</i>		<i>L. nitida</i>
<i>U. palmeri</i>		
<i>U. squamata</i>		
<i>U. stellata</i>		
<i>U. stansburiana</i> (2 spp.)		

TABLE 6. CONTINUED.

North American Desert and Plains Track (21): Group B: post-vicariant lineages	
<i>Gambelia wicklizenii</i>	<i>Rhinocheilus leconti</i>
<i>Sceloporus magister uniformis</i>	<i>Salvadora hexalepis</i> (3 ssp.)
<i>Arizona elegans</i> (3 ssp.)	<i>Sonora s. semiannulata</i>
<i>Coluber flagellum</i> (2 ssp.)	<i>Trimorphodon biscutatus</i> (2 ssp.)
<i>Pituophis melanoleucus</i> (3 ssp.)	<i>Crotalus atrox</i>

ring as allopatric species, occupying patches of relatively mesic habitats scattered sporadically down the length of the peninsula, with several lineages present on one or two Gulf or Pacific islands (e.g., *Hyla regilla*, *Eumeces skiltonianus*–*E. lagunensis*, *Elgaria multicarinata*–*E. paucicarinata*, *E. cedrosensis*, *Coluber lateralis*–*C. barbouri* and *C. aurigulus*, *Thamnophis hammondi*–*T. digueti*, *Xantusia vigilis*, and *Crotalus viridis*). The remaining lineages of this track (Table 6) do not, for the most part, occur south of 30°N latitude in Baja California. North of 30°N latitude into California and northward, and east across the Mojave Desert through Arizona, New Mexico, and south into Mexico in the Sierra Madre Occidental, these taxa demonstrate a similar pattern of allopatric distributions with many of these lineages represented by two or three species across the scope of the track (e.g., *Bufo microscaphus*; *Hyla cadaverina*, *H. regilla*–*H. exima*; *H. arenicolor*; *Elgaria multicarinata*–*E. panamintina*–*E. kingi*; *Xantusia v. vigilis*–*X. v. arizonae*, *X. h. bolsonae*, etc.; *Lampropeltis zonata*–*L. pyromelana*).

The remaining lineages included on this track (Table 6) are somewhat less clearcut in their patterns of disjunction and taxonomic/geographic correlation with the above listed taxa, but sufficient aspects of the pattern are apparent in their distributions to support their inclusion as elements of the Madrean Track.

Within the Mártir Region, elements of the Madrean Track demonstrate ecogeographic affinities coincident with the mesic habitats of the Gulf and Pacific slopes (Table 5, I, II, and IV).

Colorado Desert Track (Fig. 19)

These species have distributions coincident with the hottest and driest portions of the southwestern deserts, the area where the Mojave, Colorado, and Sonoran deserts merge. Mártir faunal

elements present on this track occur regionally only in the Colorado Desert formation (Table 5, III; Fig. 16, III). Species of the Colorado Desert Track demonstrate the most limited distributions and the lowest levels of geographic and taxonomic diversity within lineages of all the faunal assemblages described here for Baja California. Six species are included; the Colorado Desert fauna of the Mártir Region (Table 5, III), plus *Uma notata* and *Phrynosoma mcallii*.

Peninsular Range Track (Fig. 20)

Lineages of this track have their overall distributions coincident with all or much of peninsular Baja California and the Gulf of California islands, extending north along the Peninsular Range to San Geronio Pass in southern California. A few taxa of this track have radiated northeast into the Mojave Desert (e.g., *Crotalus mitchellii*, *Lichanura trivirgata*, and *Dipsosaurus dorsalis*) and southeast into the Sonoran Desert (e.g., *Lichanura trivirgata*, *Chilomeniscus cinctus*, *Phyllorhynchus decurtatus*, *Callisaurus draconoides*, *Dipsosaurus dorsalis*). Several interrelated characteristics of the lineages assigned to this track are: (1) pronounced endemism; (2) presence of most primitive extant forms; and (3) greatest levels of geographic and taxonomic diversity within lineages, all within insular and peninsular Baja California. Twenty-six species or species-complexes meet these criteria (Table 6). Twenty species-groups of the Peninsular Range Track occur in the Mártir Region (Table 5, IV), and exhibit three variations in regional distribution (Fig. 16, IVa, IVb, and IVc). Six taxa occur further south in peninsular and insular Baja California in the Central and Vizcaino deserts and the Cape Region (*Chrysemys scripta*, *Bipes biporus*, *Ctenosaura hemilopha*, *Sator* spp., *Eridiphas slevini*, and *Nerodia valida*).

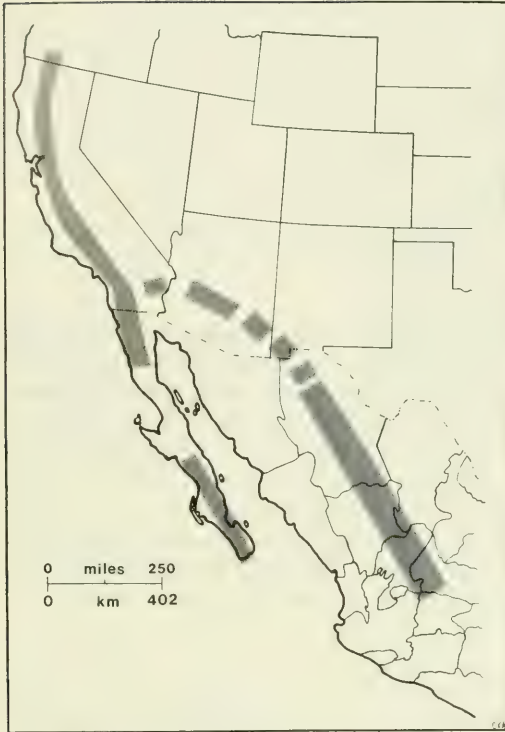


FIGURE 18. Generalized tracks of the herpetofauna of the Baja California Region: Madrean Track.

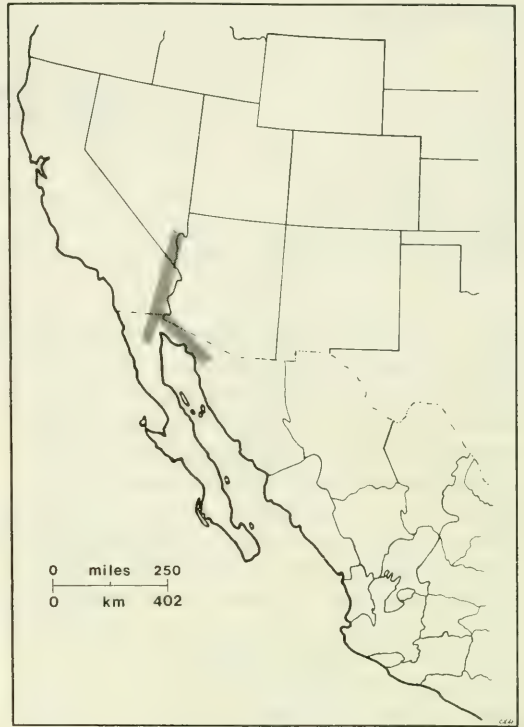


FIGURE 19. Generalized tracks of the herpetofauna of the Baja California Region: Colorado Desert Track.

North American Desert and Plains Track (Fig. 21)

Species of this track possess broad distributions throughout the North American Desert Region, and into the Great Plains Region. These species are widespread in Baja California, occurring throughout most insular and peninsular xeric habitats. The 18 taxa of the North American Desert and Plains Track present in the Mártir Region demonstrate broad ecogeographic distributions throughout the scrub and woodland habitats of the Region (Table 5; Fig. 16, V).

The lineages of this track can be divided into two subsets on the bases of distributional variations on Gulf of California islands, and the level of divergence they show within the Baja California Region as a whole: (1) those lineages that show extensive divergence within the Baja California Region, including endemic taxa on some or all of the "old islands" (Soule and Sloan 1966; see also Murphy [1983b] and Murphy and Ottley [1984]) of the Gulf of California (Table 6,

Desert and Plains Track—group A); and (2) those lineages that show little divergence throughout peninsular Baja California and are absent from the "old islands" (Soule and Sloan 1966) (Table 6, Desert and Plains Track—group B). The taxa of group A appear to have a shared evolutionary history within the Baja California Region with the lineages of the Peninsular Range Track (Table 6). The taxa of group B appear to be relatively recent (post-Pliocene) emigrants in the Baja California Region despite sharing contemporary overall continental distributions with members of group A.

Geographic diversity and endemism within the lineages of this track, when considered within peninsular and insular Baja California, are not noticeably more extensive than in other parts of the North American Region (in contrast with member lineages of the Peninsular Range Track). On the contrary, with many lineages of this track, geographic diversity and endemism are greater beyond, than within, insular and peninsular Baja California.

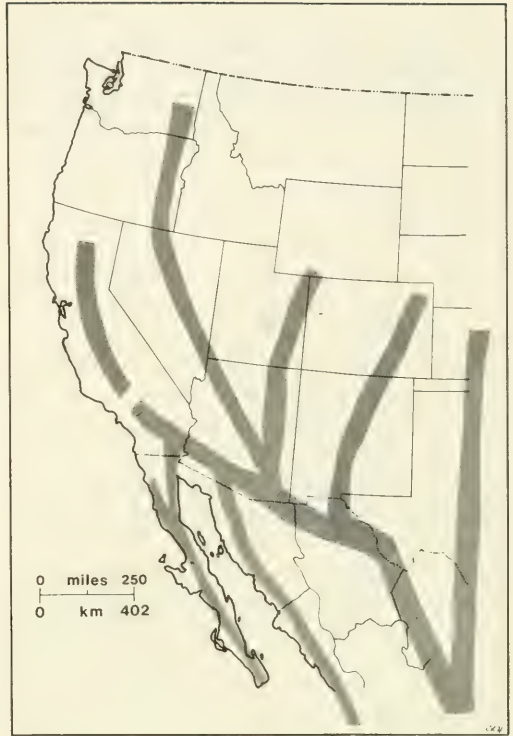
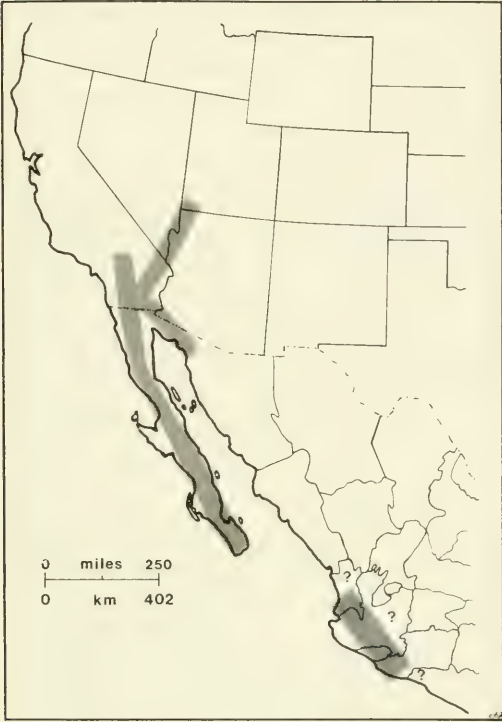


FIGURE 20. Generalized tracks of the herpetofauna of the Baja California Region: Peninsular Range Track. The extent of this track in southwest Mexico is greater than indicated, particularly southward.

FIGURE 21. Generalized tracks of the herpetofauna of the Baja California Region: North American Desert and Plains Track.

DISCUSSION

Theories on the historical biogeography of the herpetofauna of the Baja California Region have advanced on three parallel fronts: (1) with increased knowledge of contemporary herpetofaunal distributions and their ecogeographic affinities; (2) with new information about past climates and vegetation assemblages—the geofloral literature; and (3) with the advent of a new paradigm in geology—plate tectonics—depicting a dynamic rather than static landscape. Nelson (1921) and Schmidt (1922) compiled the first syntheses based on early distributional data of the peninsular biotas. Savage (1960) constructed paleoecological scenarios using data in the geofloral literature, and in conjunction with analyses of contemporary herpetofaunal distributions, presented a classic synthesis. Soule and Sloan (1966) and Savage (1967) discussed evolutionary relationships of the island herpetofaunas of the Gulf of California and proximate Pacific Ocean

islands, respectively. However, Savage and earlier investigators based their analyses on the assumption of a static or fixed peninsula, requiring Recent distributions to have been derived primarily from north to south dispersals in the case of species present on the peninsula, or temporary land bridges or chance dispersal across water barriers in the case of species present on islands.

More recently, in conjunction with developing tectonic theory, Leviton and Tanner (1960), Robinson (1973), and Smith and Tanner (1974) examined biogeographic relationships within single taxa, and indicated that particular species of the southern Baja California herpetofauna exhibit distributions more consistent with a theory of vicariant origins resulting from past tectonic events than with a theory of north to south dispersals down a fixed peninsula. Murphy (1975), following this lead, proposed a “trans-gulfian” vicariance model, based on the dislodging of pre-peninsular land masses from further south along

coastal Mexico during the Miocene, to explain contemporary distributions of many of the subtropical associated elements of the Cape Region and associated deep-water islands (*Bipes biporus*, *Nerodia valida*, *Ctenosaura hemilopha*, *Pseudemys scripta*, *Eridiphas slevini*, *Sator angustus*, *Crotalus catalinensis*, and three subspecies of *Leptotyphlops humilis*). Welsh (1976a, b, 1981) indicated that distributional data for most of the Sonoran Desert herpetofauna of Baja California showed patterns of distribution and differentiation on peninsular and insular land masses indicative of long-term isolation and evolution consistent with a tectonic vicariant origin. Elements of the herpetofauna whose distributions are consistent with this scenario include some or all members of the following genera within the Baja California Region: *Callisaurus*, *Crotaphytus*, *Dipsosaurus*, *Petrosaurus*, *Phrynosoma*, *Sauromalus*, *Sceloporus*, *Uta*, *Urosaurus*, *Coleonyx*, *Phyllodactylus*, *Cnemidophorus*, *Lichanura*, *Leptotyphlops*, *Chilomeniscus*, *Hypsiglena*, *Lampropeltis*, *Phyllorhynchus*, *Sonora*, *Tantilla*, *Trimorphodon*, and *Crotalus*. Murphy (1983a) developed a comprehensive evolutionary scenario based on geomorphological and paleobotanical evidence and tectonic theory to further elucidate the possible vicariant events responsible for many contemporary herpetofaunal distribution patterns. Kim et al. (1976), Wyles and Gorman (1978), Murphy and Papenfuss (1979), and Murphy (1983a) presented electrophoretic data that, assuming the validity of the "biochemical evolutionary clock" (Sarich 1977), support the thesis of a vicariant origin from Miocene tectonic events to account for distributional patterns among major components of the contemporary herpetofauna of Baja California.

Paleogeographic and Paleobotanic History of the Baja California Region

The following scenario is a shortened version that follows closely the synthesis developed by Murphy (1983a) but with some modifications as indicated below. Berggren and Van Couvering (1974) and Van Couvering (1978) present a geologic time scale that differs from the generally accepted time scale by placing the Miocene–Pliocene boundary at 5.2 MYBP (million years before present), rather than at 11–13 MYBP, and the Pliocene–Pleistocene boundary at 1.6–2.0 MYBP rather than at 1 MYBP. The Berggren

and Van Couvering time scale will be followed in subsequent discussion.

Miocene and Earlier

Paleogeography

The "two-fault" hypothesis of Atwater (1970), which indicates that two major migrating land masses have been active along Pacific coastal Mexico since at least the Miocene, is central to the hypothesis of a tectonic origin for many present-day herpetofaunal distributions of Baja California. Gastil et al. (1972) supported the "two-fault" theory and indicated further that "Peninsular California" was probably separated from coastal Mexico as several large fragments. These two land masses are: (1) "Alta California," defined here as consisting of present-day California from about Santa Barbara to San Francisco and west of the San Andreas fault (modified from Gastil et al. 1972), and (2) "Peninsular California," those areas south of the Transverse Ranges of southern California and west of the Gulf of California (Gastil et al. 1972). "Alta California" probably began its traverse 20–25 MYBP when it was torn from "Peninsular California" (then south of its present location, and part of coastal Mexico) from about Bahía San Sebastian Vizcaíno northward. The Pacific islands of Baja California north of Vizcaíno Bay and the Channel Islands of California are probably fragments that resulted from the traverse of "Alta California."

The dating for the separation of "Peninsular California" from coastal Mexico varies considerably from early Tertiary (60 MYBP; Gastil et al. 1972) to early Pliocene (5 MYBP; Moore 1973). Geological evidence (Atwater and Molnar 1973; Gastil and Jensky 1973) suggests that the southern end of Baja California from about La Paz south—the Cape fragment—originated from coastal Mexico near the Jalisco–Nayarit border in the mid-Miocene (12–14 MYBP). This and other separate island and island fault blocks have been simultaneously moving northwestward since mid-Miocene through Pliocene times. By the close of the Miocene, "Peninsular California" had migrated 260 km northwest to the region of the Islas Las Tres Marias (Gastil and Jensky 1973). Thus it appears that from the mid-Miocene, beginning about 14 MYBP, much of "Peninsular California" existed as an island archipelago. This archipelago included much of the present-day

Cape Region and associated deep-water islands (Santa Catalina, Santa Cruz, San Diego, and Isla Cerralvo—hereafter referred to collectively with the proto-Cape Region as the Cape Islands), as well as upland areas of the present-day Vizcaíno peninsula (possibly including Isla Cedros). Simultaneously, the northern Peninsular Ranges were beginning to uplift and separate as a result of subduction (Murphy 1983a). Murphy (1983a, fig. 6) indicated that the northern Peninsular Ranges were not totally separated from western Mexico at this time. A proto-Gulf of California was beginning to form about 14 MYBP but may not have become a permanent geographic feature until around the Miocene–Pliocene boundary, 6–5 MYBP (Gastil and Jensky 1973.)

Subduction along the fault system continued to elevate the northern Peninsular Ranges, and the central Peninsular Ranges began to emerge as a result of volcanism (Durham and Allison 1960; Karig and Jensky 1972). The Sierra Madre Occidental, the Sierra Madre Oriental, and the Mexican Plateau were also being elevated as a result of Miocene tectonic activities (King 1959). “Thus the only geographically isolated portions of the extant peninsula in the middle Miocene were the islands near (and including) the current Cape area, the Sierra Vizcaíno, and several southern peninsula-associated island localities” (Murphy 1983a). Murphy (1983a, fig. 8, and text) indicated that, by the late Miocene, the Cape Islands were connected temporarily to more northern portions of the peninsula, at least until about the Miocene–Pliocene boundary, when this connection was apparently inundated.

Paleobotany

Prior to the Eocene, neotropical floral elements dominated western Mexico; from the Eocene onward, however, declining temperatures and increasing aridity progressively restricted the neotropical-Tertiary geofloral elements southward (Axelrod 1979). Oak–pinyon woodlands and arid tropic-scrub habitats (Madro-Tertiary vegetation associations) were developing but were restricted to higher elevations of the young developing mountain regions in the interior. By the close of the Oligocene the Madro-Tertiary geoflora predominated along the mountain chains and uplands of central Mexico (Axelrod 1975). The declining temperatures and increasing arid-

ity continued to facilitate the spread of Madro-Tertiary geoflora in upland areas. Lowland areas of Mexico west of the Sierra Madre Occidental were still dominated by a neotropical flora (Axelrod 1975, 1979).

Pliocene

Paleogeography

During the Pliocene, beginning about 5 MYBP, “Peninsular California” began a more rapid northwestward movement, from the present region of the Islas Las Tres Marias to its present location (Larsen 1972; Atwater and Molner 1973; Moore 1973). The resurgence of plate interactions and the union of “Peninsular California” with the Pacific Plate (Atwater and Molner 1973) resulted in further uplift of the Peninsular Ranges. Volcanism continued in the southern Peninsular Ranges, including the Sierra de la Giganta (Mina 1957). The proto-Gulf of California had completely formed by 5 MYBP (Karig and Jensky 1972; Gastil et al. 1975) and extended from the region of the San Geronio Pass in southern California (Allen 1957) to its opening into the Pacific Ocean between the Islas Las Tres Marias and mainland Mexico (Moore 1973). In the central and southern peninsula, the Sierra Vizcaíno and possibly the Cape Islands remained isolated from the northern Peninsular Ranges. During the Pliocene the Los Angeles Basin was submerged beneath the Pacific Ocean. The combination of the flooding of the Los Angeles Basin and the formation of the proto-Gulf of California greatly reduced terrestrial access to the northern Peninsula (Durham and Allison 1960); it may have in fact been totally isolated (Murphy 1983a). Murphy (1983a, fig. 9) refers to this probable restricted or eliminated terrestrial access to the northern Peninsular Ranges as the San Geronio Barrier.

Pliocene orogenic events brought the Sierra Madre Occidental, the Sierra Madre Oriental, and the Mexican Plateau to near their present elevations (Eardley 1951; King 1959). This resulted in at least a partial barrier to gene exchange between populations of xerophilic herpetofaunas in the proto-Chihuahuan and proto-Sonoran xeric habitats on either side at the northern end of the Sierra Madre Occidental; an area referred to as the Cochise Filter Barrier (Morafka 1977).

Paleobotany

The newly formed, moderately high montane regions initiated the establishment of easterly rainshadows. Axelrod (1975) indicated that by the late Pliocene, climates in the middle latitudes (25–40°N) were essentially equivalent to those of the present. The deserts as we know them today, however, did not develop until the last interglacial period (Axelrod 1979). The only paleobotanical data from “Peninsular California” are from the Mount Eden Beds at the north end of the Peninsular Range in southern California. These are characterized by a mixture of Arcto-Tertiary and Madro-Tertiary geofloral assemblages. Eight habitats were represented: (1) desert, (2) arid subtropical scrub, (3) coastal sage, (4) grassland, (5) chaparral, (6) live oak and walnut woodland, (7) digger pine woodland, and (8) big-cone pine conifer forest (Axelrod 1937, 1950). Murphy (1983a) assumes that the desert and arid subtropical scrub habitats were marginal and that the area was predominantly mesic in character. This interpretation is supported by vertebrate fossils from the same area (Frick 1933). Terrestrial and aquatic vertebrate fossil remains from the Pliocene in southern Baja California (Miller 1977, 1980) indicate a warmer climate than the present one with year-round fresh water, possibly a subtropical savanna habitat.

Pleistocene

Paleogeography

During this epoch, the most significant process of change—from the point of view of contemporary herpetofaunal distributions—appears to have been the rise and fall in sea level resulting from glacial fluctuations that alternately isolated and then connected many islands in the Gulf of California to larger peninsular land masses (those islands separated from the peninsula by an ocean depth of less than 130 m) (Auffenburg and Milstead 1965). Tectonic events continued as well, separating the Angel de la Guarda island block (Angel de la Guarda, Partida Norte, San Lorenzo Norte and Sur) from the peninsula, prior to 1 MYBP (Moore 1973). Tectonic activity also continued the elevation of the Peninsular Ranges (Gastil et al. 1975), completing the Coast Range Corridor in California (Peabody and Savage 1958), and forcing the waters of the Gulf of California to recede to their present position. The

Sierra Vizcaíno (Minch et al. 1976) and the Cape islands (Mina 1957) were unified with the peninsula.

Paleobotany

Geofloral data from Baja California and proximate areas of the southwest from the Pleistocene indicate a progressive drying and warming trend with each of the four interglacial periods (Axelrod 1966, 1975, 1979; VanDevender and Spaulding 1979). Axelrod (1966) characterized the region at the north end of the Peninsular Ranges during the interglacials as progressing from subhumid to semiarid, to subdesert, and finally to desert environments. Increased elevation of the northern Peninsular Ranges and other mountain regions of the southwest, created easterly rainshadows that promoted increased aridity and the subsequent expansion of desert habitats during the Pleistocene (Axelrod 1979). Evidence suggests that climates in southern Baja California continued to be relatively mesic during this epoch compared with those of northern peninsular areas. A fossil Pleistocene terrestrial vertebrate fauna from southern Baja California (Miller 1977) indicates both wooded and grassland habitats occurred in the area, indicative of denser vegetations than those presently in existence. In general, excepting the evolving desert plant communities, evidence indicates that mostly minor distributional perturbations in vegetation associations, rather than significant changes in vegetational components, occurred during the Pleistocene in southwestern North America (Axelrod 1966, 1975, 1979). Such perturbations were characterized by shifts in elevation of the vegetation communities of Baja California concomitant with glacial advances and retreats in more northern areas.

The Paleobiogeography of the Herpetofauna: Previous Scenarios

The broad paleobiogeographic scenarios of Savage (1960) and Murphy (1983a) provide the most current and comprehensive framework from which to discuss the evolutionary trends of the Baja California herpetofauna. Savage (1960) and Murphy (1983a) each developed a set of pertinent data essential to an overall understanding of the evolutionary mechanisms shaping herpetofaunal relationships in Baja California. Mur-

phy's paleobiogeographic scenario, based on current understanding of plate tectonics, clearly outdates Savage's hypothesis as to the primary mechanisms shaping the peninsular herpetofaunas. However, Savage developed, in broad outline, a powerful model to describe evolving North American herpetofaunal assemblages, the progenitors of the contemporary peninsular and insular herpetofaunas. He relied on the geological history (King 1958; Durham and Allison 1960), and more particularly the paleoecological history, in his reconstruction of Tertiary and Quaternary environments. This included the geofloral history as described in the work of Chaney, Axelrod, and MacGinitie (see Murphy [1983a] or Savage [1960] for complete citations) and the concept of interdigitating and evolving geofloras. Savage's inherent assumption was that herpetofaunas evolve in conjunction with broad changes in phytogeographic relationships. He defined four contemporary herpetofaunal areas in Baja California (Savage 1960) (Fig. 2a plus the Cape Region); these areas closely approximate the four contemporary phytogeographic provinces of the peninsula as defined by Shreve and Wiggins (1964; see also this paper Fig. 2b). Savage considered each of his herpetofaunal areas to be dominated by assemblages of species with a common evolutionary history. He noted that a given Recent herpetofauna is composed of "... a compliment of species originating from several sources. A considerable portion of the species in each unit, however, originated in or near the area now occupied by the faunal assemblages. For these reasons, present-day herpetofaunas are mixtures of species of diverse historical origins, although a particular fauna is dominated by derivatives of one of the historical elements defined" (Savage 1960:189).

Murphy (1983a:14) challenged the assumption that particular herpetofaunas evolved in conjunction with and parallel to particular geofloras. His argument is supported by two examples that illustrate the absence of complete distributional correlation between groups of herpetofaunal species and particular contemporary vegetational associations of Madre-Tertiary vegetation in Baja California. These arguments are weak and based on a few rigid and very exacting applications of what was intended only to be a very general correlation. An exact correlation between a particular vegetational associa-

tion (e.g., the Sonoran Desert flora) and a particular herpetofauna (e.g., the Colorado Desert herpetofauna) was never assumed, intended, or implied in my understanding of Savage's model. Savage did not rule out the possible ameliorating effects of physiography or of interspecific competition, for example, in determining distribution. He used the evolving geofloras as evidence of existing paleoclimatic conditions and in so doing made the assumption only that contemporary and phylogenetic antecedent herpetofaunal assemblages occupy similar climatic regimes. This seems a valid assumption considering the taxa concerned are terrestrial ectotherms and have physiological limitations that translate directly into ecogeographic restrictions (Bartholomew 1958). This assumption also seems well supported by the fossil record. Murphy's arguments are further weakened by the fact that throughout his own paleobiogeographic scenario, he employs the same paleobotanical literature and makes the same general assumption that geofloras are evidence of paleoclimatic conditions that are indicative of certain historical herpetofaunal assemblages in a given region during a given time.

Generalized Tracks and Ecogeographic Patterns

The strength of Murphy's (1983a) presentation lies in the excellent paleobiogeographic synthesis he constructs to explain contemporary distribution patterns, and in the genetic evidence he presents to support many of his conclusions. However, I find his herpetofaunal assemblages ("tracks") to have serious shortcomings. Apparently this is a result of his misapplication of the concept of track (Croizat 1964), and the concomitant lack of distinction between contemporary distribution patterns and the diverse historical assemblages from which they derived.

It is important to clarify some terms and concepts critical to subsequent discussion. Murphy (1983a) describes six herpetofaunal areas in peninsular Baja California: Californian, Colorado Desert, Vizcaíno Desert North, Coastal Vizcaíno Desert, Peninsular Area (with three subdivisions), and the Cape Area. These herpetofaunal areas are basically broad phytogeographic units defined on the basis of major physiographic or geomorphological transformations and concomitant differences in the general botanical com-

position (based on Nelson 1921; Savage 1960; Shreve and Wiggins 1964; Bostic 1971; Loomis et al. 1974; and Murphy's own fieldwork). They are comparable in concept to ecogeographic formations (Fig. 14), but lack as fine a resolution because they each encompass a larger geographic area containing complex geomorphological formations with numerous vegetational communities. They are probably best characterized as ecogeographic provinces.

Murphy (1983a) compiles the herpetofaunal composition of these ecogeographic provinces and compares them quantitatively. From this analysis, he derives what he terms "tracks." He then states "phylogenetic relationships of the herpetofaunal elements are then superimposed on these tracks of distribution to suggest hypotheses explaining the evolutionary relationships of the herpetofauna of Baja California" (Murphy 1983a:3). The use of the term "track" in this sense is misleading and confusing. The original concept of "track" as developed and employed by Croizat (1964; see also Croizat et al. 1974; Craw 1983; Craw and Weston 1984) has two components. The first concept is that of the individual track; this concept depicts the spatial (geographical) expression of relatedness among disparate forms. The geographic distributions of all related forms of a given taxon (e.g., a species complex, members of a genus or family) from disparate geographic areas, when considered together and depicted spatially, comprise an individual track. The second concept, that of generalized or standard track (op. cit.) describes the phenomenon of congruency in space of more than one individual track. Both individual and generalized tracks are spatial expressions of evolutionary time. A generalized track, because of the spatiotemporal congruency it expresses, indicates historical homology among the individual tracks, and thus among the life forms represented. In other words, a generalized track is a spatial and temporal representation of a group of phylogenetically unrelated organisms that shared proximate space through time, or a common evolutionary history.

Murphy states (1983a:11): "I re-emphasize that among the various species constituting each of these five major generalized tracks of distribution, some have phylogenetic affinities with tropical Mexico and others with territories north and east of the peninsula." In my understanding of

Croizat (1964), for unrelated life forms to be members of the same generalized track, they need to demonstrate distributional similarities throughout much or all of their respective ranges. In other words, one would find consistent spatial overlap among the phylogenetic lineages of each of the various member taxa of the generalized track. From the lack of this spatial overlap among represented lineages, one would have to conclude the presence of more than a single generalized track. Murphy's (1983a) use of the term "track" to describe herpetofaunal taxa that have present-day geographic overlap within Baja California, but lack such spatial congruency among their respective phylogenetic lineages elsewhere, is inconsistent with the concept of track.

The common denominator supporting Murphy's faunal groupings is consistent spatial overlap among species, geographic or ecologic, or both, only within parts of Baja California. Lacking the requisite geographic congruency among represented lineages beyond the Baja California Region, one would have to conclude that these groupings represent contemporary ecogeographic patterns, not historical patterns or tracks. They appear to be analogous with the heretofore described ecogeographic patterns of the herpetofauna of the Sierra San Pedro Mártir Region of northern Baja California (Fig. 16; Table 5; and text).

Subsequent use of the term track in this discussion should be understood in the sense used by Croizat (1964). When indicating Murphy's "tracks" quotation marks will be used to distinguish his from the generalized tracks that this investigation indicates exist among the herpetofauna of the Baja California Region. Savage's (1960) historical assemblages appear to be consistent with the temporal aspect of generalized tracks; these parallels will be indicated below. I consider his spatial designation of province consistent with the spatial aspects of generalized tracks, however, like Morafka (1977) I consider Savage's (1960) provinces to equal superprovinces. I follow Morafka (1977) in my use of province to indicate a geographical unit with uniform dominant physiography, vegetation, and fauna (see Dice 1943). My use of the term track, in the spatial sense, is synonymous with province or superprovince as indicated.

The terms track and generalized track, as used in the temporal sense and assemblage or histor-

ical assemblage, are used interchangeably and indicate historical biogeographic groupings; they represent events in evolutionary time. The term fauna is used to indicate a contemporary grouping of forms with similar ecogeographic restrictions; a province or track in the spatial sense may include one or more faunas but only a single fauna is considered the participant fauna (Morafka 1977). The terms fauna and track as used in the spatial sense represent the present, in ecological time; here considered to be subsets of the historical groupings.

Extant Faunas and Generalized Tracks

Savage (1960) did not list all of those species or species-groups he considered to have evolved together as part of a particular historical assemblage. But, using his examples of species with distributions representative of his historical assemblages, the list of extant vegetational associations occupied by Recent derivatives of his historical complexes and components, and the contemporary species composition of Savage's Herpetofaunal Areas, I assigned each contemporary species to a particular historical assemblage. The assignment of species and species-groups, though based on Savage's (1960) work, is my own interpretation and is thus subject to errors for which I alone am responsible. Murphy likewise did not list the member species for each of his nine possible "tracks," leaving the reader to decipher from his table 2 (Murphy 1983a) those species that fit the description for each of his "minor" and "major generalized tracks." He was unclear about proper assignment of some forms (e.g., on page 6, he assigns the *Sceloporus magister* complex, minus the nominal species, to his "Transpeninsular Mesophilic Track," but on page 32 he discusses this complex as part of his "Transpeninsular Xerophilic Track"). I have attempted to interpret Murphy's work and assign species in accordance with his descriptions; once again I alone am responsible for any errors.

The following hypothesis of interacting and overlapping generalized tracks comprising the contemporary herpetofauna of the Baja California Region is a working one that best integrates our current knowledge from pertinent fields. However, it is a hypothesis to be tested and changed wherever future investigations find it lacking.

The Generalized Tracks of the Baja California Herpetofauna

Savage's (1960) and Murphy's (1983a) Californian Herpetofaunal Area (Fig. 2a), consisting of the Pacific Slope of Baja California north of latitude 30°N, is the most biologically complex area of the Mártir Region, and probably of the entire peninsula. It is also one of the most poorly investigated by previous workers. Savage indicated that this area was dominated by an assemblage of species with more extensive ranges northward in coastal and montane California that shared an evolutionary history associated with derivatives of the Madro-Tertiary geoflora (the Californian Component of his Madrean Complex). In addition, he indicated that some elements of his Sonoran Desert Component of the Desert and Plains Complex occur within the Californian Area. This study indicates that elements of four contemporary faunas (High Sierran Scarps, Californian, Peninsular Range, and North American Ubiquitous Scrubland; Fig. 15, 16; Table 5), representing four different tracks (Pacific Northwest, Madrean, Peninsular Range, and North American Desert and Plains; Fig. 17, 18, 20, 21), overlap on the Pacific Slope of Baja California north of latitude 30°N.

The Californian Fauna together with the High Sierran Scarps Fauna (Table 5, I and II) match closely the species Savage indicated as endemic to and dominating the Californian Herpetofaunal Area. Several species within this area, as noted by Savage, are associated primarily with derivatives of the Arcto-Tertiary geoflora. These species, the High Sierran Scarps Fauna, are restricted to Arcto-Tertiary floral derivatives in northern Baja California and southern California. However, outside of Baja California, members of this fauna demonstrate broader ecological niches and occur in conjunction with more mesophilic derivatives of the Madro-Tertiary geoflora (see Species Accounts; Stebbins 1966, 1985). The variability in niche breadth in different parts of their range, and the presence of sympatric congeners within the Baja California Region, suggest that the geographic limits of the High Sierran Scarps Fauna result from competition. Overall distributions of these species closely match those of the Californian Fauna, suggesting that these two faunas have a very similar and perhaps parallel evolutionary history in western North

America. The relatively low Coefficient of Difference and high Similarity Coefficient and Community Coefficient values (Table 4; Fig. 15) between areas occupied by these two faunas are also indicative of a close relationship. With the exception of three species of the Californian Fauna (*Rana aurora*, *Bufo boreas*, and *Clemmys marmorata*) that are also associated primarily with Arcto-Tertiary geofloral derivatives, the species of the High Sierran Scarps Fauna and the Californian Fauna are considered to be contemporary members of the Madrean Track (Fig. 18; Table 5, 6; and below).

The Pacific Northwest Track

Rana aurora, *Bufo boreas*, and *Clemmys marmorata* are considered to be members of the Pacific Northwest Track (Fig. 17; Table 5, 6). This track is synonymous with Savage's Western American Complex of the Old Northern Element. Pacific Northwest Track members have the most tenuous toehold on the predominantly xeric Baja California peninsula. Several member species occur in scattered populations in a few canyons of extreme northwestern Baja (i.e., *Aneides lugubris* and *Ensatina eschscholtzii*). Members of this track probably dispersed into the Region following completion of the Coast Range Corridor (Peabody and Savage 1958) during the cooler and moister Pleistocene epoch. Two of these species, *Rana aurora* and *Bufo boreas*, appear to have derived from Asian forms, and as noted by Savage (1960), apparently dispersed across the Bering Land Bridge and down the west coast of North America during the Pleistocene (Savage's Holarctic Element). It is reasonable to propose that they constitute a second, more recent generalized track, one that overlaps the older Pacific Northwest Track.

The Madrean Track

The Madrean Track (Fig. 18; Table 6) is considered synonymous, in terms of process and pattern, with Savage's (1960) Madrean Complex of the Young Northern Element, but with a considerably different species composition. Savage distinguished a Californian Component and a San Lucan Component in his Madrean Complex. His San Lucan Component includes most of the species here assigned to the Peninsular Range Track (Table 6), as discussed below. Included as

contemporary elements of a San Lucan component of my Madrean Track (Table 6) are only those forms present as sibling species in the Californian and Cape regions (and on some Pacific coastal islands of Baja California) and absent from most or all of the Central and Vizcaíno deserts (e.g., *Eumeces*, *Hyla*, *Elgaria*, and *Coluber* "lateralis complex").

Savage (1960) considered his Madrean Complex the oldest assemblage in the Baja California Region. Such dating probably refers to those taxa that are here assigned to the Peninsular Range Track fauna (Table 6). Distribution of populations on "old" or "deep-water" islands of the Gulf of California (Soule and Sloan 1966; Murphy 1983b), and the concomitant relatively greater levels of divergence within lineages (see Species Accounts for taxonomic references), indicate that the members of the Peninsular Range Track are much older elements on the land masses of Baja California than are Madrean Track forms. Biochemical and electrophoretic analyses (Kim et al. 1976; Wyles and Gorman 1978; Murphy and Papenfuss 1979; Murphy 1983a) indicate a probable mid-Miocene divergence for several of the lineages of the Peninsular Range Track.

The Madrean Track fauna, both within and beyond the Baja California Region, appears to be a previously more widespread, vicariated (see Figure 18) assemblage of relatively mesophilic species-groups. The level of differentiation among disjunct populations of these forms within the Baja California Region appears to match Mayr's (1978) criteria for sibling species or semispecies. Divergence and endemism within lineages of Madrean Track elements beyond Baja California (in California, Arizona, New Mexico, and Mexico) are considerably greater than the level of sibling species, with most lineages having populations along the track that appear to meet the criteria of superspecies (Mayr 1978). The relatively greater differentiation within lineages of the Madrean Track beyond, compared to within Baja California, suggests a long-term historical relationship among these species-groups prior to their inhabiting Baja California, and an evolutionary history distinct from, yet probably paralleling, the lineages of the Peninsular Range Track.

Much of existing Baja California appears to have been inaccessible to southward emigration of terrestrial vertebrates (see Paleobiogeographic

History above), possibly from the mid-Miocene and probably from about the Miocene–Pliocene boundary until the Pleistocene. If so, after the mid-Miocene or the Miocene–Pliocene boundary and prior to the Pleistocene, Madrean Track elements could have reached Baja California only by being carried along on the migrating land masses, i.e., by “transgulfian vicariance” (Murphy 1975, 1983a). The complete absence of Madrean Track forms on the “old” or “deep-water” Gulf islands (Soule and Sloan 1966; Murphy 1983a, b; Murphy and Ottley 1983, 1984) discounts this possibility, although vicariance and subsequent extinction cannot be entirely ruled out. An alternative possibility is that some of these lineages were present on the proto-northern Peninsular Range land masses during the Miocene and vicariated at a later time (e.g., Miocene–Pliocene boundary) than did lineages on the Cape Islands. However, the relatively low levels of divergence between the Baja California populations of these lineages, their absence from the “old” or “deep-water” Gulf islands, and the increase in numbers of Madrean Track species present along a south to north transect in peninsular Baja California, strongly suggest a relatively recent (i.e., Pleistocene) diffusion—gradual movement across hospitable areas over long periods (Pielou 1979)—southward. The disjunct distributions (vicariance) of some Madrean Track elements along the peninsula suggests even more recent (mid-Pleistocene to Recent) fragmentation of ranges in conjunction with climatic shifts toward aridity (Axelrod 1967, 1975, 1979) or from possible periodic inundation of low-lying areas by changes in sea level, or both (Flint 1971).

At least two possible scenarios are suggested by the distributions of the Madrean Track lineages within Baja California. Firstly, the spatial relationships between the congeners of the Californian and the High Sierran Scarps Faunas (Table 5), which I propose to have resulted from competition, are consistent with a hypothesis of Pleistocene to Recent periodic diffusions by these lineages southward into Baja California. Late Pliocene or Pleistocene formation of a terrestrial connection between Baja California and southern California land masses and the concomitant orogenic uplift would have provided southward emigration routes as well as the upland retreats consistent with the contemporary distributions of these faunas. These contemporary distribu-

tions of mesophilic species, and those of more xerophilic species associated with other tracks discussed below, indicate that for at least part of this time, barriers to gene flow existed. Elements of the Madrean Track probably dispersed in successive diffusions across a partial or fluctuating barrier (San Geronio Barrier) during this time. Secondly, prior to this time, from mid-Miocene to Pleistocene, it is unclear what the nature of the terrestrial connection at the northern end of the extant peninsula was, or even if it existed. Some elements I have assigned to the Madrean Track have distributions that suggest they may have been present on the northern peninsular land masses at mid-Miocene, when increased tectonic activity vicariated their ranges, isolating them from ancestral stocks to the east (e.g., *Anniella geronimensis*, *Cnemidophorus labialis*, and *Xantusia henshawi*).

A hypothesis that incorporates both possible scenarios is preferred. Species like *Anniella geronimensis*, *Cnemidophorus labialis*, and *Xantusia henshawi* are not good candidates to support a Pleistocene diffusion hypothesis; their endemism, narrow niches, and low vagility are all indicative of species that are evolutionarily relatively conservative, with their present ranges probably contracting rather than expanding. They appear to be the remains of an ancestral fauna, a proto-Madrean Track fauna that may have vicariated in the Miocene. If this were indeed the case, these species could arguably be evidence of another, earlier, generalized track, possibly the result of the same geomorphological events that shaped the Peninsular Range track further south as discussed below. On the other hand, their sympatric congeners and the other species of the Madrean Track, probably made their appearance in the northern peninsula (and beyond), subsequent to Pleistocene climatic changes, sea level shifts, and related phenomena that promoted an ingress across the San Geronio Barrier. Under the cool moist conditions of Pleistocene glacial maxima, the more hydrophilic High Sierran Scarps Fauna could have undergone diffusion southward. The presence of *Lampropeltis zonata* and *Batrachoseps pacificus* on Todos Santos Island off the Pacific coast of Baja California supports the contention that cool, moist conditions were more widespread in northern Baja California in the past. With glacial retreat and the long-term drying and warming trend culminating in

the late Pleistocene to Recent (Axelrod 1967, 1975, 1979), conditions became increasingly favorable for the westward and southward dispersal of the warm-mesophilic Californian Fauna. Concomitant with these southward advances of the Californian Fauna, the High Sierran Scarps Fauna was increasingly restricted and relegated to habitats at higher, cooler elevations. With the advancing aridity, even the Californian Fauna became restricted; ranges became fragmented and populations in arid areas relegated to protect microhabitat, such as their present-day riparian corridor distributions at lower elevations in the Mártir Region (Table 5; Fig. 16). This scenario of diffusing and fragmenting faunas is consistent with the current evidence of geologic and climatic conditions during Pleistocene and Recent times. It is also consistent with and supportive of the thesis that sympatry within monophyletic lineages is evidence of dispersal (Croizat et al. 1974; Platnick and Nelson 1978).

Four interrelated criteria were used to distinguish species of the Madrean Track from those of the Peninsular Range Track (discussed below). (1) Madrean Track species and species groups, for the most part, exhibit extensive ranges beyond the Baja California Region. Members of the Peninsular Range Track have their greatest, and in many cases their total, distribution within the Baja California Region. (2) In the Baja California Region, Madrean Track forms have comparatively less differentiation within monophyletic lineages compared to lineages of the Peninsular Range Track, on both peninsular and insular land masses. (3) Madrean Track forms are present only on some of the land-bridged islands (Soule and Sloan 1966; Murphy and Ottley 1983, 1984) of the Gulf of California and on some of the Pacific coastal islands of Baja California and California. They are absent from all of the "old" or "deep-water" islands (Soule and Sloan 1966; Murphy and Ottley 1983, 1984) of the Gulf, which are inhabited by numerous endemic forms of the Peninsular Range Track lineages and some elements of the North American Desert and Plains Track (discussed below). (4) As a general trend, Madrean Track forms appear to have their closest relationships within monophyletic lineages with forms occurring in California, Arizona, New Mexico, and the northwest central uplands of Mexico (e.g., *Rana boylii* [Zweifel 1955], *Lampropeltis zonata* [Tanner

1953], *Batrachoseps* [Wake 1966b], *Xantusia* [Bezy 1972; Bezy and Sites 1987]). Peninsular Range Track elements are most closely related to forms occurring in lowland areas from central Mexico southward (e.g., *Ctenosaura hemilopha* [Bailey 1928; Smith 1972], *Eridiphas* [Duellman 1958; Leviton and Tanner 1960; Cadle 1984; Dowling and Jenner 1987], *Phyllodactylus* [Dixon 1964, 1969; Murphy and Papenfuss 1979], *Cnemidophorus hyperythrus* and *C. ceralbensis* [Lowe et al. 1970; Robinson 1973], *Phrynosoma coronatum* [Presh 1969], *Sator* [Wyles and Gorman 1978], *Nerodia* [Conant 1969], and *Bipes* [Kim et al. 1976; Papenfuss 1982]).

Peninsular Range Track

The third contemporary fauna with elements in Savage's Californian Herpetofaunal Area of the Mártir Region is the Peninsular Range Fauna (Table 5, IV). Some of these taxa occur also in the Colorado Desert Herpetofaunal Area (Fig. 2a) and southward, throughout the length of the peninsula. The Peninsular Range Fauna is part of the larger Peninsular Range Track (Table 6; Fig. 20) comprised primarily of forms endemic to the Baja California Region and associated with warm-temperate and subtropical floral elements. Many forms of the Peninsular Range Track occur only south of the Mártir Region in the Central and Vizcaíno deserts, in the Cape Region, or on islands in the Gulf of California (see Murphy 1983a; Murphy and Ottley 1983, 1984).

These peninsular and insular endemics are the oldest lineages present in the Baja California Region, dating from mid-Miocene (Murphy 1983a). Savage (1960) indicated the members of this fauna were part of two of his southward dispersing waves: a Sonoran Component of his Desert and Plains Complex, and a Madrean Complex. However, the present distributions of these species and species-groups are more consistent with a theory of origin in Baja California based on vicariance, each distribution appearing—at least in part—to result from the migration and fragmentation of peninsular and insular land masses from coastal Mexico. Murphy (1975) proposed such a theory of vicariated origin to account for several of these lineages found in the Cape Region and on some associated islands; his "trans-gulfian migration" hypothesis. Welsh (1976a, b, 1981)

proposed a similar hypothesis to account for the distributions of most of the Sonoran Desert-associated lineages of Baja California (see list at beginning of Discussion), that are considered to have a shared evolutionary history with the more clearly vicariated subtropical Cape Island endemics of the Peninsular Range Track. Murphy (1983a) included these Sonoran Desert-associated lineages and added several more mesophilic lineages in his revised "trans-gulfian vicariance" model.

Murphy (1983a) included the mesophilic lineages *Batrachoseps*, *Hyla* (= *H. regilla* progenitor), *Eumeces*, and *Elgaria* in his "trans-gulfian vicariance" model. Exception is taken to the addition of these lineages, all of which are herein considered to be part of the Madrean Track. In adding these mesophilic genera, Murphy (1983a) assumed that the Cape Region or Cape Islands supported both Neotropical and Madro-Tertiary geofloral elements during the mid-Miocene when the area became separated from coastal Mexico: "In the absence of fossil data, I assume that the Cape Islands supported a mixture of Neotropical-Tertiary and Madro-Tertiary geofloras in the respective tropical and temperate climatic regimes; the temperate regime of the Cape resulting from altitudinal effects" (Murphy 1983a:16). Murphy was making the same kind of assumption (inferring presence of historically associated herpetofauna from presence of geoflora) that he criticized Savage for making. Despite his apparent contradiction, and "willingness" to join Savage and myself in making this kind of assumption, I think in this particular case, the assumption is invalid as I shall discuss below.

Axelrod (1979:28) indicated the presence of both Neotropical geofloral elements (dry tropic forest and arid tropic scrub) and Madro-Tertiary geofloral elements (oak-pinyon woodland) along coastal western Mexico during the Miocene. However, he stated that "... woodland presumably reached southward down a line of volcanos, linking the flora of the Cape Region with that of Sonora-Sinaloa-Nayarit-Jalisco, which probably lived above scattered dry-tropic forest and thorn forest" (1979:29). Whereas it seems possible that volcanism could have provided the requisite upland habitat in some parts of coastal western Mexico as Axelrod indicated, the Cape Islands land masses are areas of granitic batholith, not volcanic rock (Mina 1957; Gastil et al. 1975).

Furthermore, there is no evidence that this area had been uplifted to sufficient height by mid-Miocene to create the cooler climatic regime requisite for the Madro-Tertiary geoflora.

Even in the event that such vegetational elements existed at the right time and in the right place on the geomorphic progenitors of the Cape Islands, these vegetation communities would have been present on upland areas as islands of habitat surrounded by great expanses of Neotropical floral elements (Axelrod 1979:28). As such, (a) these "islands" would have been far removed from the northwest central highland and central plateau areas of Mexico considered to be the centers of differentiation and evolution of the Madro-Tertiary geoflora (Axelrod 1975, 1979), and (b) they would also most probably be highly depauperate. Therefore, it seems highly unlikely that these "islands" could contain and support the mesophilic elements of the ancestral herpetofauna that are thought to have evolved in association with the then-developing Madro-Tertiary vegetation.

The possibility that *Batrachoseps*, *Hyla*, *Eumeces*, and *Elgaria* vicariated on the Cape Islands in upland habitats during mid-Miocene cannot be entirely discounted. However, it seems highly improbable and less likely than the more parsimonious explanation that these genera are elements of the Madrean Track (Fig. 18), whose origins in the Cape Region are probably, as Savage (1960) suggested, the result of late Pliocene or Pleistocene diffusions down an existing peninsula.

The fossil herpetofaunal evidence that exists from the Cape Region (Miller 1977) dates from the late Pliocene and includes *Boa*, *Geochelone*, and *Crocodylus*, etc., indicating decidedly tropical conditions at least in the vicinity of this lowland site.

The noninsular forms of the Peninsular Range Track show three general patterns of distribution in the Baja California Region: (1) restricted endemic lineages—those lineages found only in one or more of the four southern ecogeographic provinces (Murphy 1983a) of the peninsula or on associated "deep-water" islands (Soule and Sloan 1966; Murphy 1983b), or both; generally south of latitude 28°N through the Cape Region (e.g., *Bipes biporus*, *Chrysemys scripta*, *Ctenosaura hemilopha*, *Sator* complex, *Nerodia vallida*, and *Eridiphas slevini*); (2) endemic lineages (note:

some of these lineages have member-species that when considered separately, fit the description in (1) above)—those lineages that range throughout most or all of the Peninsular Ranges but not north of the San Geronio Barrier (e.g., *Cnemidophorus hyperythrus*, *Crotaphytus insularis*, *Petrosaurus* complex, *Phyllodactylus* complex, *Sceloporus magister* complex—those members with $2n = 30$ chromosomes, *Sceloporus orcutti* complex, *Elaphe rosaliae*, *Crotalus enyo*, and *C. ruber*); (3) radiated lineages—those lineages that have expanded beyond the Peninsular Ranges into habitats of the Mojave and Sonoran deserts and north and east (*Callisaurus draconoides*, *Coleonyx switaki*, *Dipsosaurus dorsalis*, *Phrynosoma coronatum*, *Sauromalus* complex, *Chilomeniscus* complex, *Crotalus mitchellii*, *Lichanura trivirgata*, and *Phyllorhynchus decurtatus*).

Murphy (1983a) outlined a plausible paleobiogeographic scenario to account for the distributional permutations and divergence within lineages among the Peninsular Range Track fauna. Lineages with member elements distributed in accordance with each of the above described geographic patterns consist of sibling species along the peninsula, with one or two forms in the Cape Region and another form or forms to the north across the Isthmus of La Paz (e.g., *Petrosaurus*, *Urosaurus*, *Sceloporus orcutti* complex, *S. magister* complex, *Phyllodactylus* complex, and *Chilomeniscus* complex). Murphy attributed this species-pairs phenomenon to a temporary or fluctuating terrestrial corridor between the Cape Islands (Region) and areas to the north, probably during the late Miocene or early Pliocene (see his "Transpeninsular Xerophilic Track"). It would appear that more than a single vicariating event, or intermittent gene flow between more than two areas is involved here, based on the presence of more than two distinct forms among several of these lineages on the southern peninsula. Murphy (1983a, b) gives detailed accountings of the numerous unique patterns among insular distributions of the lineages of the Peninsular Range Track, and also for those insular-occurring forms I have assigned to the North American Desert and Plains Track (see Table 6 and below).

Assuming the validity of the hypothesis that species of the Peninsular Range Track predate—in Baja California—those species of the Madrean Track, then future electrophoretic or immuno-

logical distance data should indicate a trend of greater genetic distance between Peninsular Range Track members and their southwest Mexican siblings, than that which would be found between the Madrean Track forms and their siblings beyond the Baja California Region (with the exception of some of the possible proto-Madrean Track forms like *Cnemidophorus labialis* and *Xantusia henshawi*). Good (1988) presented allozyme data for the genus *Elgaria* that indicate a closer relationship between *E. paucicarinata* of the Cape Region and *E. panamintina* of southeastern California, than between *E. paucicarinata* and *E. kingi* of western Mexico. Following Savage's (1960) scheme of historical herpetofaunas of North America, the lineages of the Peninsular Range Track would be called the Peninsular Range Complex of the Young Northern Herpetofauna.

The Colorado Desert Track

Peninsular members of the Colorado Desert Track (Fig. 19; Table 6) are found only in the Colorado Desert Herpetofaunal Area (Fig. 2a). The Colorado Desert was formed during the Pleistocene; it resulted from the continued elevation of the northern Peninsular Ranges, which forced the Gulf of California to recede (Atwater and Molner 1973), and the accumulation of alluvial deposits from the Colorado River filling in the head of the Gulf (Norris 1958). Species of the Colorado Desert Track have the most restricted distributions of the xerophilic herpetofauna of the Baja California Region; monophyletic lineages demonstrate the lowest levels of interpopulational morphological differentiation.

The limited distributions and minimal intralinear differentiation (see Adest 1977), together with their endemism, suggest a Pleistocene to Recent isolation and in situ evolution for these forms. The presence of congeners of several of these species among the Peninsular Range Track fauna (Table 6), suggests that competition may limit the spread of these species further south into other desert habitats of Baja California.

This is an incipient track and hence does not demonstrate the characteristics of spatial and temporal fragmentation among forms associated with older tracks (except see the distribution of the genus *Uma*; Stebbins 1985). The Colorado Desert Track becomes apparent when one ex-

amines the pattern of distributions of sibling forms in the Chihuahuan, Sonoran, and Peninsular deserts. In fact, these four desert areas, each considered here as a generalized track with its own participant fauna, can also be viewed as subsets of the more extensive and older North American Desert and Plains Track (see below).

Morafka (1977:187) hypothesized a faunal assemblage associated with the Colorado Desert he called the California Gulf Arch Assemblage. He considered this assemblage of 10 reptiles (*Dipsosaurus dorsalis*, *Sauromalus obesus*, *Callisaurus draconoides*, *Lichanura trivirgata*, *Chilomeniscus cinctus*, *Chionactis occipitalis*, *Phyllorhynchus decurtatus*, *Crotalus cerastes*, *Crotalus mitchellii*, and *Gopherus agassizii*) to be a secondary, more northerly centered ecological unit of the Sonoran Herpetofauna, a fauna centered to the south in Sonora and Sinaloa, Mexico. I agree that the fauna of the Colorado Desert show strong affinities with the Sonoran Herpetofauna, but I do not consider it a subset thereof. Despite the distributional similarities apparent among these forms, track analysis indicates this is a synthetic assemblage. It appears to me that his California Gulf Arch Assemblage is comprised of Peninsular Range and Sonoran herpetofaunal elements that have radiated into amenable habitats not otherwise occupied in each of the other areas, plus Colorado Desert Track forms that have evolved in situ; in both cases as a result of post-Pleistocene geomorphological and climatic changes favoring expansion of extreme desert habitats.

Adest (1987) analyzed allozyme data for *Callisaurus draconoides* from populations in the Cape Region of Baja California throughout much of the range including Nevada, and down the west coast of Mexico to the vicinity of Mazatlán. His results indicated low genetic diversity throughout the range, with some minor differences in populations near Mazatlán and on Isla Cerralvo in the Gulf of California. His data were inconclusive to resolve the question of a Pleistocene isolation in either a Sonoran or a Cape Region refugium (Savage 1960) or a California Gulf Arch refugium (Morafka 1977). However, he concluded that his data did not support a model of a Pleistocene Cape Region refuge for the species. Unfortunately he did not include samples from the population on Isla Angel de La Guarda, a deep-water island isolated from central peninsular Baja California 1 MYBP (Murphy 1983b).

Significant differences between this population and those tested by Adest (1987) would add credence to a hypothesis of a mid-latitude peninsular or insular refuge for *Callisaurus draconoides*.

Following Savage's historical groupings, the species of the Colorado Desert Track might be called the Colorado Desert Component of the Desert and Plains Complex.

The riparian herpetofauna of the Colorado River delta region (*Bufo alvarius*, *Bufo cognatus*, *Bufo woodhousei*, *Urosaurus ornatus*, *Thamnophis marcianus*, and *Trionyx spiniferus*) were not included in my ecogeographic analysis because none of them range south into the Mártir Region. With the exceptions of *Bufo alvarius* and *Urosaurus ornatus*, which have distributions characteristic of Sonoran Track forms, these species appear to be post-Pleistocene to Recent radiations from the east. *Trionyx spiniferus* and *Bufo woodhousei* appear to be elements of a western radiation of the Austriparian Herpetofauna (Savage 1960) centered in the southeastern U.S. *Thamnophis marcianus* appears to be a member of the Chihuahuan Track that has crossed the Cochise Filter Barrier (Morafka 1977), and *Bufo cognatus* appears to be a member of the North American Desert and Plains Track.

The North American Desert and Plains Track

The North American Desert and Plains Track (Fig. 21) overlaps four less extensive herpetofaunal tracks: the Peninsular Range Track, the Colorado Desert Track, the Sonoran Desert Track (encompassing parts of northern Sinaloa, Sonora, and southern Arizona), and the Chihuahuan Desert Track (including much of Mexico's central plateau—see Morafka 1977). Each of these tracks has an endemic herpetofauna, however these tracks also share many species and species-groups. As here employed, the term North American Desert and Plains Track encompasses the combined areas and fauna common to the Peninsular Range Deserts, Colorado Desert, Sonoran Desert, and Chihuahuan Desert generalized tracks, and extends into the high deserts and plains of the southwest, west, and central North America. This concept of an older (relative to the true desert tracks listed above), more comprehensive arid regions track is consistent with Morafka's (1977) concept of a Miocene-Pliocene "Moha-

via" Biota, and the Desert and Plains super-province of Savage (1960).

The fauna of the North American Desert and Plains Track occurs within all of both Savage's and Murphy's herpetofaunal areas of Baja California. Elements of this ubiquitous fauna appear to have populated the Baja California Region by two distinct means:

(1) The majority of these lineages (Table 6, North American Desert and Plains Track, group A) apparently accompanied the progenitors of the lineages of the Peninsular Range Track, having vicariated on prepeninsular and insular land masses as they were separated from coastal Mexico in the mid-Miocene. These species and species-groups are widely distributed on the "old" or "deep-water" islands of the Baja California Region and they all demonstrate relatively high degrees of morphological differentiation within monophyletic lineages on the peninsula and associated islands (Soule and Sloan 1966; Savage 1967; Ballinger and Tinkle 1972; Case 1975; Murphy 1983*a, b*; Murphy and Ottley 1983, 1984).

(2) Other elements (Table 6, North American Desert and Plains Track, group B) dispersed southward along the peninsula after Pleistocene to Recent climatic changes, which promoted corridors of xeric habitats at the northern end of the Peninsular Ranges, allowing for diffusion southward. Evidence for this diffusion hypothesis are the relatively low levels of morphological differentiation among all peninsular and insular populations of each lineage, and their exclusive occurrence on land-bridged islands of the Gulf of California and on some apparently recently isolated land-bridged islands of the Pacific side of the peninsula (Soule and Sloan 1966; Savage 1967; Ballinger and Tinkle 1972; Case 1975; Murphy 1983*b*; Murphy and Ottley 1983, 1984). These recently invading ubiquitous xeric forms could be considered as a distinct, overlapping generalized track analogous to the situation with the earlier Old Northern Element and the more recent, overlapping Holarctic Element on the Pacific Northwest Track. These more recent lineages might be considered a Holxeric Element of the Desert and Plains Track.

The hypothesis for the evolution of the North American Desert and Plains Fauna, proposed by Savage (1960), incorporates three distinct centers of evolution of xerophilic herpetofauna of North

America. Dispersal and genetic introgression between these areas since the late Pleistocene and possibly during glacial minima has resulted in the present, relatively continuous distribution of much of this fauna. The endemic xerophilic herpetofaunas of the Peninsular Range Track, the Sonoran Desert Track, and the Chihuahuan Desert Track appear to be comprised of those forms with a competitive disadvantage in xeric habitats, such as restricted niches, or lower vagility, or both.

SUMMARY

Theories of the historical biogeography of the the herpetofauna of the Baja California Region have developed in conjunction with the growing geofloral literature and the development of a new paradigm in geology, that of plate tectonics. Past syntheses by Schmidt (1922), Savage (1960), and Murphy (1983*a*) reflect this evolution of ideas. Five primary historical patterns or generalized tracks are proposed to describe the interaction of historical faunal assemblages that produced contemporary distributional patterns: the Pacific Northwest Track, the Madrean Track, the Peninsular Range Track, the Colorado Desert Track, and the North American Desert and Plains Track. Vicariance of peninsular land masses from western Mexico as a result of Miocene-Pliocene tectonic activity is the most significant process shaping extant patterns. In situ evolution during the Pliocene, Pleistocene, and Recent epochs, as well as radiations northward from these southern vicariated areas, and biotic dispersal—both diffusion and secular migration (Pielou 1979)—from proximate regions to the north and east played major secondary roles influencing present distributional patterns.

RESUMÉN

Conduje un análisis ecogeográfico de la herpetofauna de la región de San Pedro Mártir en Baja California Norte, México. Se analizaron más de 3,000 archivos municipales conseguidos de la literatura, los museos, y investigaciones en el campo, por medio de una matriz de formaciones ecogeográficas basadas en los climas regionales, la fisiografía, y la vegetación existente. Métodos numéricos y intuitivos de análisis biográfico indican que las 65 especies que se encuentran ocurren en siete distintos modelos de distribución.

Se analizan estos modelos contemporáneos en un contexto geográfico más amplio para encontrar indicaciones de sus orígenes históricos.

Se han desarrollado las teorías de la biogeografía histórica de la herpetofauna de la región de Baja California en junto con la creciente literatura geoflora y el desarrollo de un nuevo paradigma de la geología—el de “plate tectonics.” Síntesis anteriores por Schmidt (1922), Savage (1960), y Murphy (1983a) reflejan esta evolución de ideas. Se propone cinco patrones históricos, o “generalized tracks” (Croizat 1964) para describir la interacción de “faunal assemblages” históricos que producen los modelos de distribución contemporáneos: el “Pacific Northwest Track,” el “Madrean Track,” el “Peninsular Range Track,” el “Colorado Desert Track,” y el “North American Desert and Plains Track.” La “vicariance” (Croizat et al. 1974) de tierras peninsulares del oeste de México como resultado de actividad tectónica es al proceso más significativo en el porceso de la formación de los modelos que existen hoy día. Evolución en situ durante las épocas Pliocena, Pleistocena, y Reciente, además de radiaciones hacia el norte de estas áreas “vicariated” del sur, y “biotic dispersal” (diffusion and secular migration—Pielou 1979) de las regiones vecinas del norte y el este tomaron importantes papeles secundarios que influyeron los modelos de distribución que existen ahora.

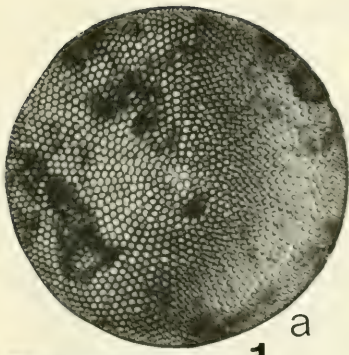
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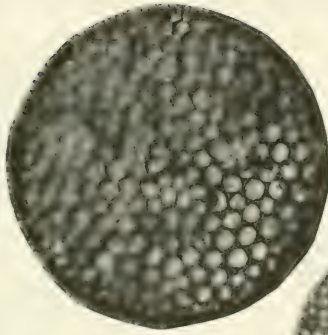
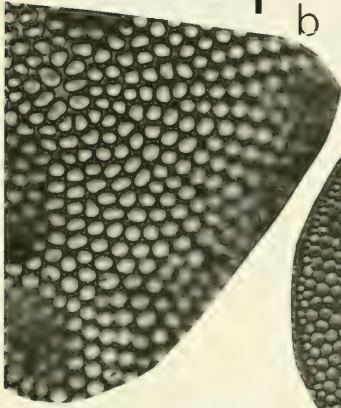
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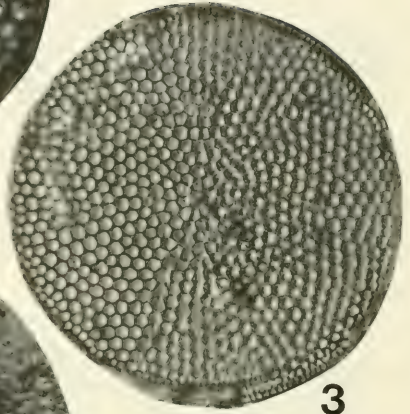
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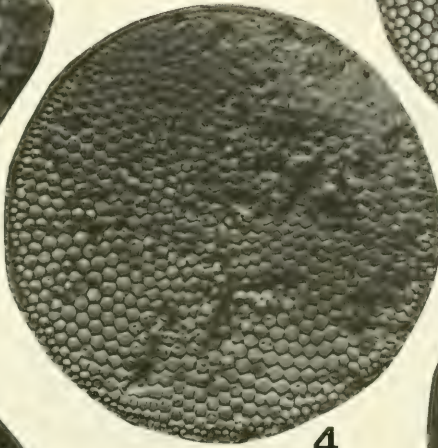
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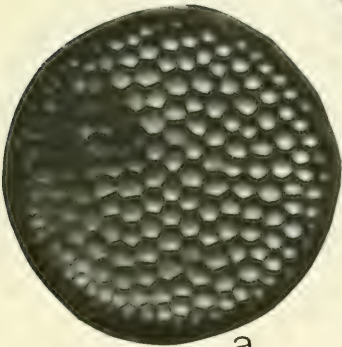
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4



5



6 a
b



7



8 a



b



Plate 7

FIGURE:

1. *Thalassiosira lacustris* (Grunow) Hasle; D = 60 μm ; a: focus up, b: focus down, c-f: margin showing tubular processes.
2. *Thalassiosira lacustris* (Grunow) Hasle; D = 29 μm .
3. *Coscinodiscus nitidus* Gregow; D = 25 μm .
4. *Cyclotella pygmaea* Pantocsek; D = 13 μm .
5. *Cyclotella striata* (Kutzing) Grunow; D = 32 μm .
6. *Cyclotella striata* (Kutzing) Grunow; D = 20 μm .
7. *Cyclotella comta* (Ehrenberg) Kutzing; D = 30 μm .

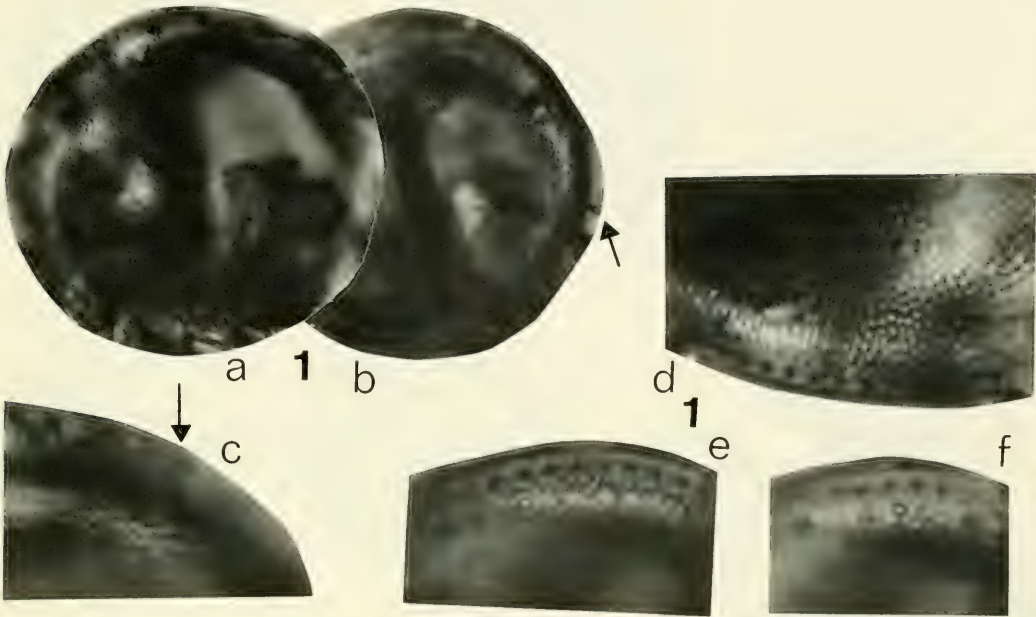


Plate 8

FIGURE:

1. *Actinocyclus normanii* (Gregory) Hustedt; D = 46 μm .
2. *Actinocyclus normanii* (Gregory) Hustedt; D = 43 μm .
3. *Actinocyclus normanii* (Gregory) Hustedt; D = 49 μm .
4. *Actinocyclus normanii* f. *subsalsa* (Juhlin.-Dannt.) Hustedt; D = 23 μm .
5. *Actinocyclus normanii* f. *subsalsa* (Juhlin.-Dannt.) Hustedt; D = 27 μm .
6. *Actinocyclus normanii* f. *subsalsa* (Juhlin.-Dannt.) Hustedt; D = 18 μm .
7. *Actinocyclus normanii* (Gregory) Hustedt; D = 45 μm .
8. *Actinocyclus normanii* f. *subsalsa* (Juhlin.-Dannt.) Hustedt; D = 17 μm .
9. *Actinocyclus normanii* (Gregory) Hustedt; D = 32 μm .
10. *Actinocyclus normanii* f. *subsalsa* (Juhlin.-Dannt.) Hustedt; D = 22 μm ; arrow shows pseudonodule.
11. *Actinocyclus normanii* (Gregory) Hustedt; D = 44 μm .
12. *Actinocyclus normanii* (Gregory) Hustedt; D = 48 μm ; a, b: focus down, shows pseudonodule(s)?; b: marginal focus, enlargement; c: entire valve, focus down; d: focus up; e: focus down, marginal focus, shows striate margin.

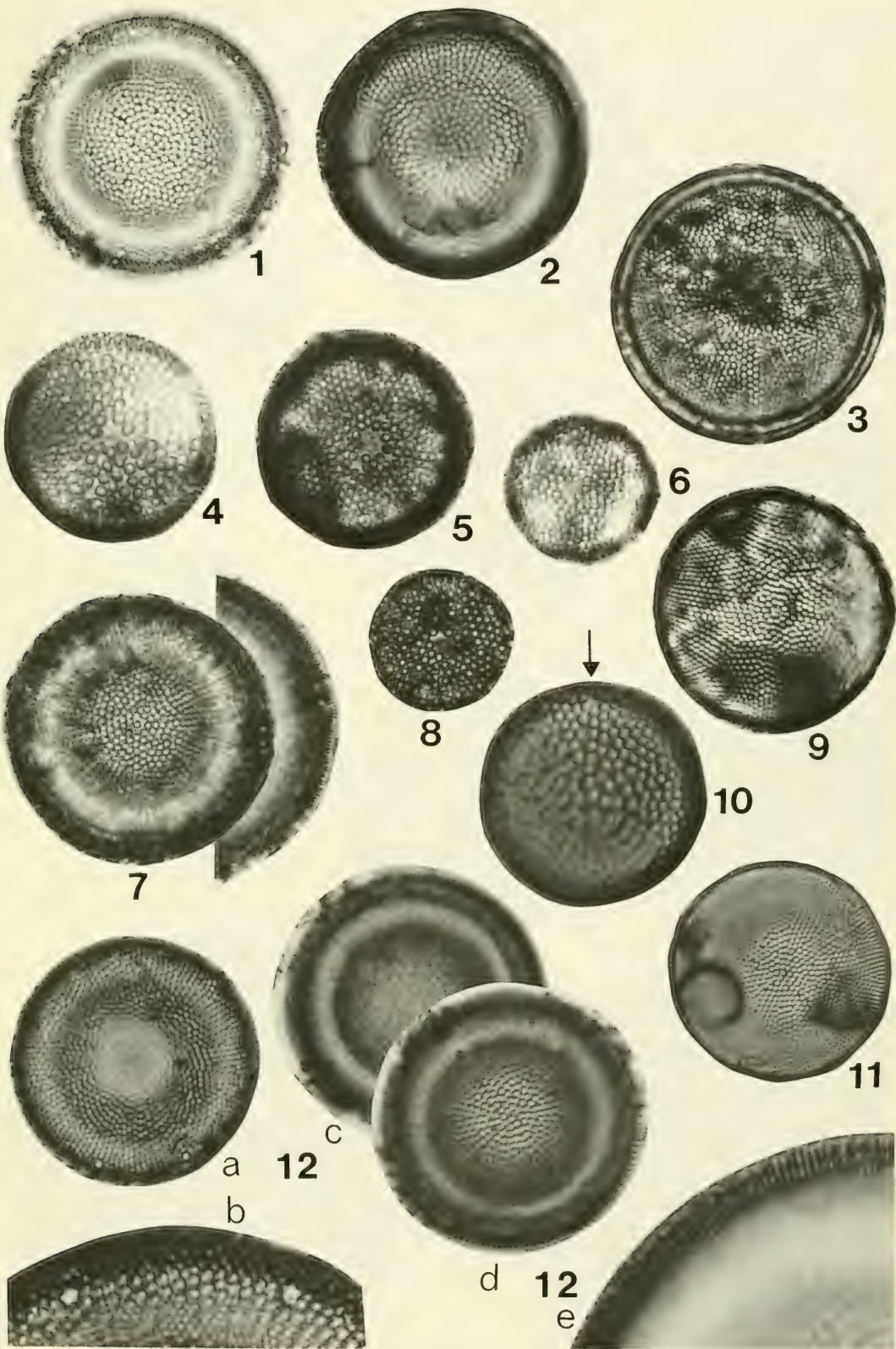


Plate 9

FIGURE:

1. *Actinocyclus octanarius* Ehrenberg; D = 72 μ m; a: marginal enlargement, b: entire valve; c: dark field.
2. *Actinocyclus?* sp. 1; D = 28 μ m.
3. *Coscinodiscus curvatulus* Grunow; D = 64 μ m.
4. *Coscinodiscus curvatulus* Grunow; D = 88 μ m.
5. *Actinocyclus octanarius* Ehrenberg; D = 96 μ m.
6. *Thalassiosira* sp. 1; D = 26 μ m; a: focus down, b: focus up.
7. *Thalassiosira punctigera* (Castracane) Hasle; D = 85 μ m.
8. *Thalassiosira punctigera* (Castracane) Hasle; D = 115 μ m.

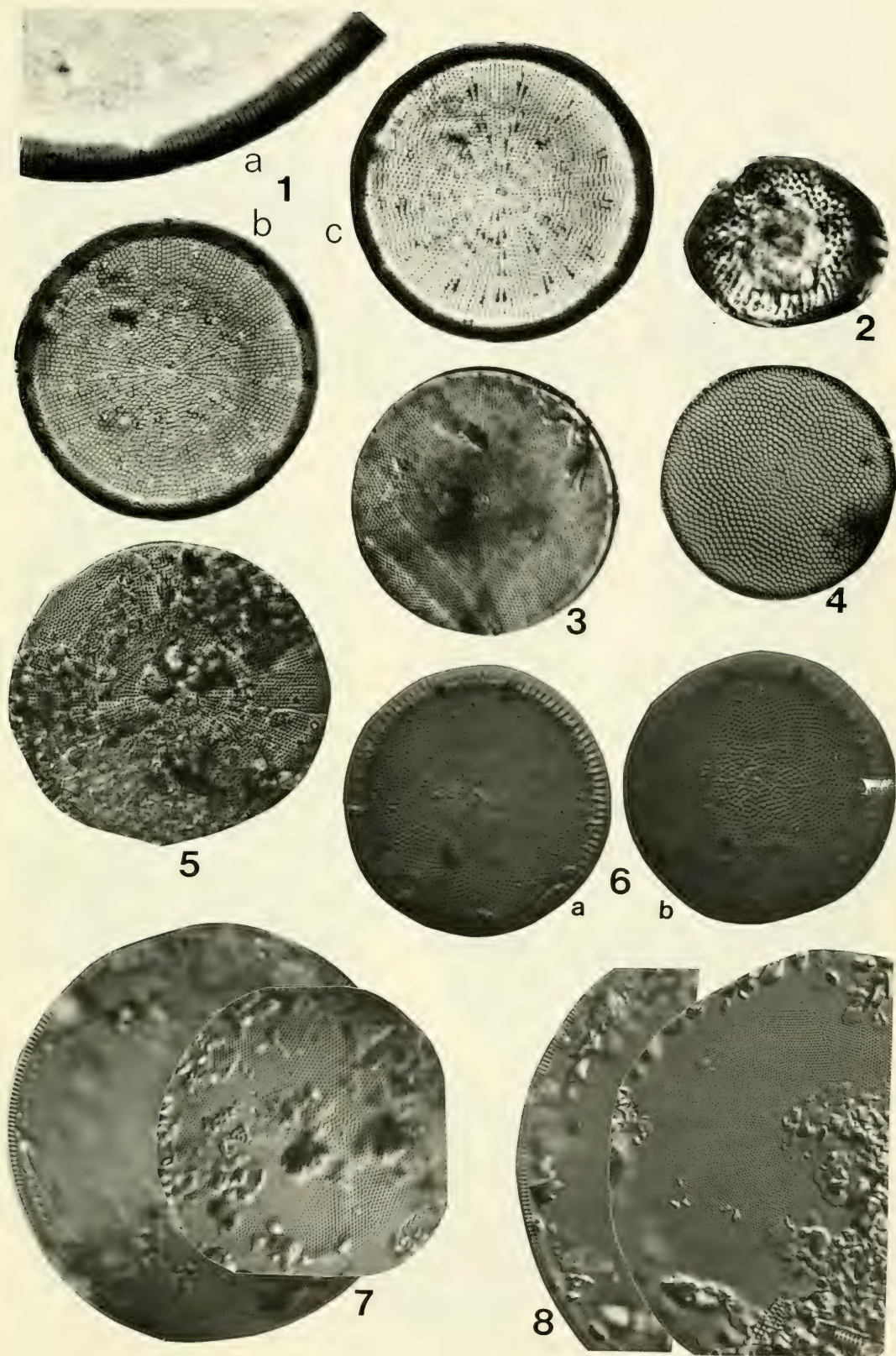


Plate 10

FIGURE:

1. *Thalassiosira nodulolineata* (Hendey) Hasle and Fryxell; D = 50 μm ; a: entire valve, b: central area and marginal enlargement, c: focus down, d: dark field.
2. *Thalassiosira hendeyi* Hasle and Fryxell; D = 68 μm ; a: entire valve, b: central area and marginal enlargement, arrows show processes.
3. *Thalassiosira hendeyi* Hasle and Fryxell; D = 30 μm .
4. *Thalassiosira hendeyi* Hasle and Fryxell; D = 27 μm ; a: focus down, b: focus up.
5. *Thalassiosira hendeyi* Hasle and Fryxell; D = 28 μm .
6. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 46 μm .
7. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 48 μm .

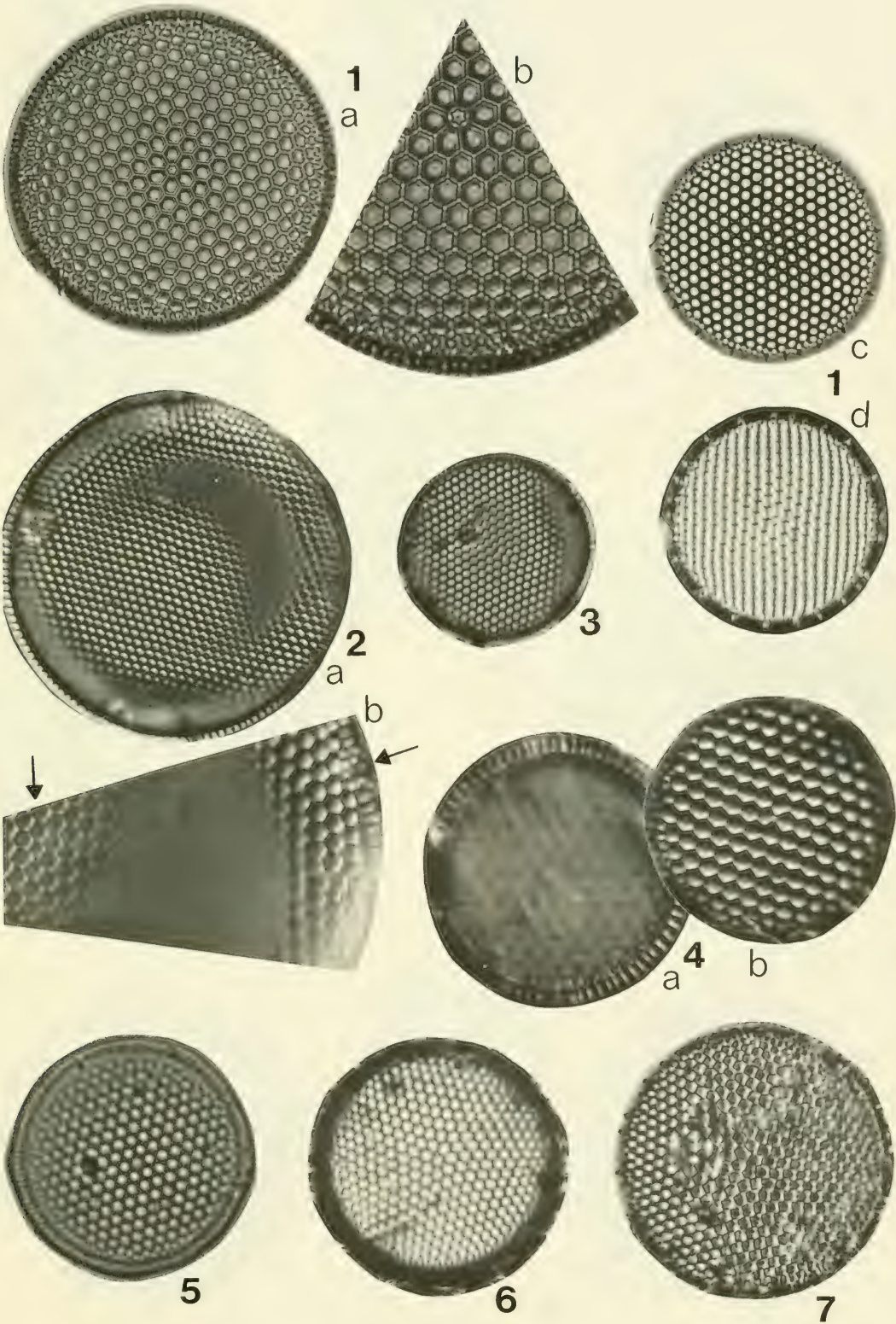
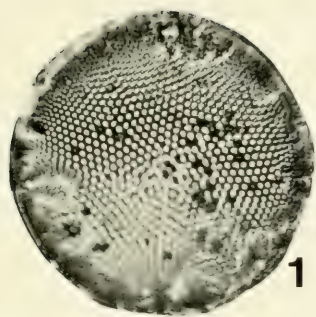


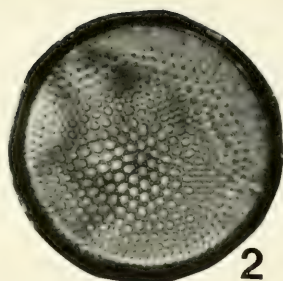
Plate 11

FIGURE:

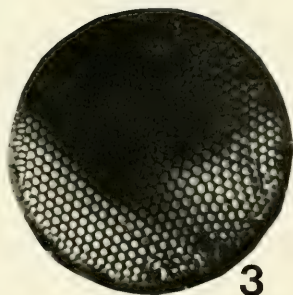
1. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 40 μ m.
2. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 33 μ m.
3. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 45 μ m.
4. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 66 μ m; a: entire valve, b: central area and marginal enlargement.
5. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 42 μ m; a: entire valve, b: central area and marginal enlargement, note tubular process at 3 o'clock.
6. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 36 μ m.
7. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 53 μ m.
8. *Thalassiosira eccentrica* (Ehrenberg) Cleve; D = 34 μ m.
9. *Thalassiosira* cf. *T. pacifica* Gran and Angst; D = 72 μ m.



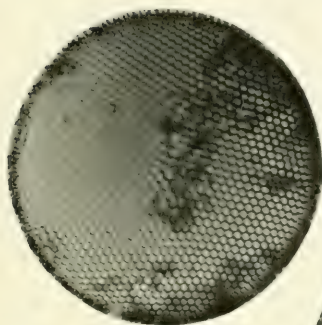
1



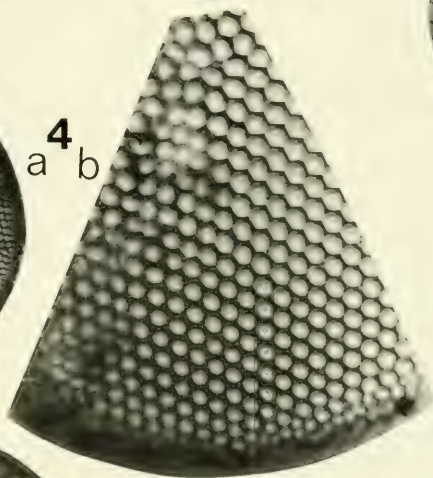
2



3

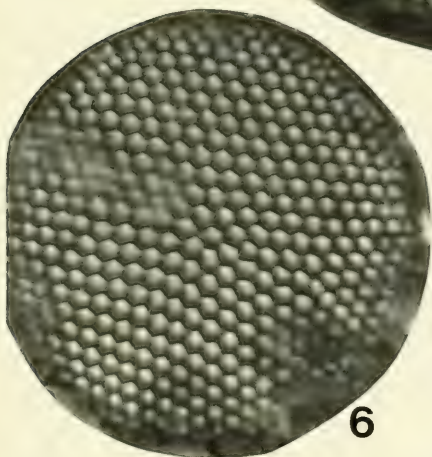


4
a b

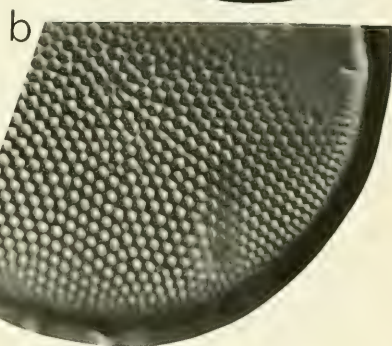


a

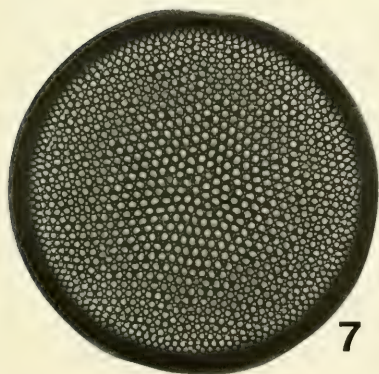
5



6



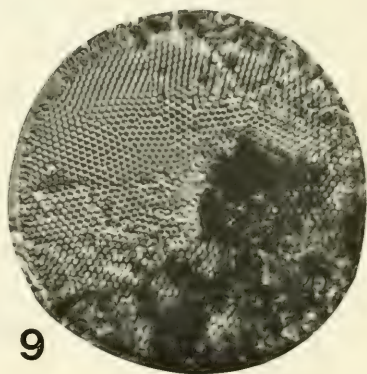
b



7



8



9

Plate 12

FIGURE:

1. *Thalassiosira decipiens* (Grunow) Jorgensen; D = 32 μ m; a: focus up, b: focus down.
2. *Thalassiosira decipiens* (Grunow) Jorgensen; D = 27 μ m.
3. *Thalassiosira decipiens* (Grunow) Jorgensen; D = 40 μ m; a, focus up, b, focus down.
4. *Thalassiosira decipiens* (Grunow) Jorgensen; D = 21 μ m; a: focus down, b: focus up.
5. *Thalassiosira decipiens* var. 1; D = 14 μ m; a: focus down, b: focus up.
6. *Thalassiosira decipiens* var. 1; D = 16 μ m.
7. *Thalassiosira decipiens* var. 1; D = 11 μ m.
8. *Thalassiosira decipiens* var. 1; D = 15 μ m; a: focus down, b: focus up.
9. *Thalassiosira decipiens* var. 1; D = 14 μ m; a: focus down, b: focus up.
10. *Hyalodiscus scoticus* (Kutzing) Grunow; D = 96 μ m.
11. *Hyalodiscus scoticus* (Kutzing) Grunow; D = 88 μ m.
12. Genus and species indeterminate; L = 15 μ m.

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APPENDIX A. COLLECTING STATIONS IN THE SIERRA SAN PEDRO MÁRTIR REGION, BAJA CALIFORNIA NORTE, MÉXICO.

Station number	Name and coordinates	Elevation		Primary vegetation*
		ft	m	
1	San Matías Pass; 31°19'N, 115°30'W	3,200	980	CBS
2	Valle de Picacho; 31°15'N, 115°35'W	3,400	1,004	CBS
3	Rancho El Burro; 31°14'N, 115°36'W	4,450	1,360	P-J
4	Cañón Esperanza (mouth); 31°12'N, 115°27'W	1,640	500	CBS
5	Valle de San Felipe (center); 31°12'N, 115°20'W	1,575	480	CBS
6	Cañón Copal (mouth); 31°09'N, 115°25'W	1,970	600	CBS
7	San Telmo; 31°08'N, 116°05'W	400	120	CDS
8	Arroyo León (head); 31°08'N, 115°31'W	7,400	2,260	Conifer
9	San Antonio del Mar; 31°07'N, 116°17'W	75	23	CDS
10	Arroyo de San Rafael, 6 mi E MS Rancho; 31°07'N, 115°33'W	5,000	1,525	P-J, Chp
11	Mikes Sky Rancho; 31°06'N, 115°38'W	4,150	1,270	Chp
12	Cerro Venado Blanco; 31°06'N, 115°29'W	9,325	2,820	Conifer
13	Cañón Copal (head); 31°06'N, 115°29'W	7,375	2,225	Conifer
14	Arroyo de San Rafael, 2 mi E MS Rancho; 31°05'N, 115°37'W	4,350	1,330	Chp
15	Arroyo de San Rafael (head); 31°05'N, 115°31'W	7,275	2,210	Conifer
16	Cañón del Diablo, 2 mi W mouth; 31°05'N, 115°24'W	2,500	760	CBS
17	Cañón del Diablo (mouth); 31°05'N, 115°22'W	2,175	660	CBS
18	Mikes Sky Rancho, airstrip; 31°04'N, 115°38'W	4,600	1,400	Chp
19	Rancho Concepción; 31°04'N, 115°34'W	4,775	1,450	Chp
20	Cañón del Diablo, 4 mi W mouth; 31°04'N, 115°24'W	2,675	810	P-J/CBS
21	Cañón del Diablo, 6 mi W mouth; 31°03'N, 115°24'W	3,150	960	P-J/CBS
22	Observatorio Nacional de México; 31°02'N, 115°27'W	9,200	2,800	Conifer
23	Cañón del Diablo, 8 mi W mouth; 31°02'N, 115°24'W	4,000	1,220	P-J
24	Compamento Forestal; 31°01'N, 115°28'W	8,100	2,460	Conifer
25	Yerba Buena Spring; 31°00'N, 115°28'W	8,000	2,420	Conifer
26	Vallecitos, SE end; 30°59'N, 115°28'W	8,000	2,420	Conifer
27	Rancho San Jose; 30°58'N, 115°25'W	2,300	640	CSS
28	Socorro; 30°58'N, 115°40'W	4,200	1,280	CSS/Chp
29	Oak Pasture; 30°58'N, 115°36'W	5,900	1,830	Chp
30	Los Llanitos; 30°58'N, 115°26'W	7,900	2,410	Conifer
31	Picacho Spring; 30°58'N, 115°25'W	8,200	2,500	Conifer
32	Blue Bottle Mt.; 30°58'N, 115°24'W	9,675	2,950	Conifer
33	Rancho Viejo trail head, La Tasajera ridge; 30°57'N, 115°30'W	7,900	2,410	Conifer
34	Llanitos Camp; 30°57'N, 115°26'W	7,700	2,350	Conifer
35	La Jolla; 30°56'N, 115°35'W	5,250	1,600	Chp
36	La Tasajera Ridge, 2 mi NE R. Viejo; 30°56'N, 115°28'W	7,000	2,120	Conifer
37	Rancho Viejo; 30°55'N, 115°29'W	6,900	2,200	Conifer
38	San Antonio Creek, 1 mi W La Grulla; 30°54'N, 115°30'W	6,750	2,060	Conifer
39	La Grulla, W end; 30°54'N, 115°29'W	6,800	2,080	Conifer
40	La Grulla, center; 30°54'N, 115°27'W	6,900	2,100	Conifer
41	La Encantada Creek; 30°54'N, 115°26'W	7,050	2,150	Conifer
42	Arroyo San Antonio, head; 30°53'N, 115°30'W	6,575	2,000	Conifer
43	La Grulla, SE end; 30°53'N, 115°26'W	6,950	2,110	Conifer
44	La Encantada; 30°53'N, 115°25'W	7,100	2,160	Conifer
45	Arroyo Valladares, Santa Cruz Road; 30°52'N, 115°43'W	2,025	620	CSS
46	Cañón El Cajón (mouth); 30°52'N, 115°14'W	2,125	650	CBS
47	El Alcatraz; 30°51'N, 115°26'W	6,800	2,080	Conifer
48	Cañón El Cajón, 6 mi W mouth; 30°51'N, 115°16'W	4,000	1,220	P-J/CBS
49	Rancho San Antonio; 30°50'N, 115°38'W	1,970	600	CSS
50	El Remudero; 30°50'N, 115°22'W	6,900	2,200	Conifer
51	Cañón Barrosa/Cañón El Cajón divide; 30°50'N, 115°17'W	6,575	2,000	P-J
52	Cowpod Camp, Cañón El Cajón; 30°50'N, 115°16'W	5,200	1,580	P-J
53	Cañón Barrosa (head); 30°49'N, 115°19'W	7,550	2,300	Chp
54	Valle de Chico (center); 30°49'N, 115°08'W	1,575	480	CBS
55	Santa Rosa; 30°48'N, 115°21'W	6,800	2,080	Conifer
56	Mission San Pedro Mártir; 30°47'N, 115°24'W	5,500	1,675	Chp
57	Santo Tomás; 30°46'N, 115°24'W	5,900	1,800	Chp

APPENDIX A. CONTINUED.

Station number	Name and coordinates	Elevation		Primary vegetation*
		ft	m	
58	Arroyo Alonso (head); 30°46'N, 115°20'W	6,575	2,000	Conifer
59	Cañón Agua Caliente, 9 mi W mouth; 30°41'N, 115°16'W	3,125	950	CBS
60	Cañón Agua Caliente, 4 mi W mouth; 30°40'N, 115°12'W	2,225	680	CBS
61	Cañón Auga Caliente (mouth); 30°40'N, 115°09'W	2,200	670	CBS
62	Rancho Rosarito; 30°28'N, 115°18'W	2,750	840	CSS/CBS
63	Rio de Rosarito; 30°21'N, 115°22'W	2,200	670	CDS
64	San Juan de Dios; 30°11'N, 115°09'W	2,175	660	CDS
65	Rancho El Metate; 30°11'N, 115°08'W	2,200	670	CDS

* Key to vegetations: Conifer = Coniferous Forest, CSS = Coastal Sage Scrub, CBS = Creosote Bush Scrub, CDS = Central Desert Scrub, Chp = Chaparral, and P-J = Pinyon-Juniper Woodland.

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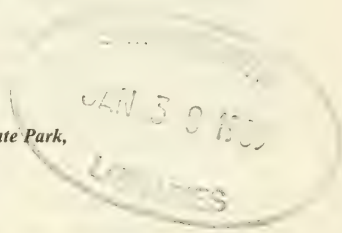
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THREE NEW SPECIES OF *HOLOGRAPHIS* (ACANTHACEAE)
FROM MEXICO

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ABSTRACT: Three new species of *Holographis*, *H. caput-medusae*, *H. leticiana*, and *H. tolantongensis*, are described from Mexico. Diagnostic features of each species are illustrated and the known distribution of the three species is mapped. A revised key to the entire genus, incorporating data and species that have become known since the last monograph of *Holographis*, is presented. Fifteen species are now known for this entirely Mexican genus.

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INTRODUCTION

Holographis Nees is a small genus of perennial herbs and shrubs endemic to Mexico. Since my monograph of the genus (Daniel 1983), in which 10 species were recognized, one species (*H. peloria*) has been transferred into *Holographis* from *Stenandrium* Nees (Daniel 1984) and an additional species (*H. websteri*) has been newly described (Daniel 1986). Continued botanical exploration in the dry forests of Mexico has revealed the existence of three undescribed and distinctive species, bringing the total number of species now known for the genus to 15. These three new species are described below.

Because of the increased botanical activity in Mexico in recent years, a significant number of

additional collections of previously recognized species of *Holographis* has become available. Some species (e.g., *H. argyrea*, *H. anisophylla*, and *H. parayana*) are now known from twice as many or more collections than they were in 1983. Fruiting collections have been located for four species (*H. argyrea*, *H. anisophylla*, *H. peloria*, and *H. pueblensis*) whose capsules and seeds were previously undescribed. The known geographic distributions of several species (e.g., *H. anisophylla* and *H. peloria*) have been increased. A key to all species of the genus is presented below that includes the five taxa recognized in *Holographis* since the monograph of 1983 and that incorporates information from other species based on additional collections examined.

KEY TO THE SPECIES OF *HOLOGRAPHIS*

1. Leaves opposite (rarely subopposite).
2. Corolla yellow with maroon markings, vertical during anthesis, the upper lip 1-2.5 mm long; stamens 1.5 mm long with thecae 1-1.3 mm long; style 4 mm long; Balsas basin in Guerrero. *H. argyrea*

2. Corolla white or pinkish, horizontal during anthesis, the upper lip 2.5–5 mm long; stamens 2.8–5.5 mm long with thecae 1.5–2.5 mm long; style 5–7.5 mm long; plants occurring to the north of Guerrero.
3. Abaxial surface of bracts, bractlets, and calyx glabrous; calyx 4–5 mm long; corolla white; Tamaulipas. *H. tamaulipica*
3. Abaxial surface of bracts, bractlets, and calyx pubescent; calyx 5–10 mm long; corolla pinkish; plants occurring to the south and west of Tamaulipas.
4. Corolla glabrous on external surface; calyx lobes aristate at apex; staminode 2 mm long; Hidalgo. *H. tolantongensis*
4. Corolla pubescent on external surface; calyx lobes acute at apex; staminode 0.5–0.8 mm long; Sonoran Desert region. *H. virgata*
1. Leaves whorled, four per node (lower leaves of *H. pueblensis* sometimes opposite to subopposite; rarely opposite on some, but not all, shoots of individuals of *H. ehrenbergiana*).
5. Leaves orbicular, 0.8–1.3 times longer than wide, the margin spinose toothed; bracts alternate; Chihuahuan Desert region. *H. ilicifolia*
5. Leaves lanceolate to ovate to elliptic to obovate to oblanceolate, 1.5–6 times longer than wide, margin entire to undulate; bracts opposite; plants occurring outside of the Chihuahuan Desert region.
6. Corolla yellow, the upper lip 6–9 mm long; stamens 9–11 mm long; seeds glabrous.
7. Inflorescence to 4.5 cm long, many-flowered; bracts 5–11 mm long, 1.5–2 mm wide; calyx 7–10.5 mm long. *H. pueblensis*
7. Inflorescence to 2 cm long, usually reduced to 2 flowers; bracts 1.5–5 mm long, 0.5–1 mm wide; calyx 3.5–6.5 mm long. *H. ehrenbergiana*
6. Corolla white, pinkish, or reddish (color unknown in *H. hintonii*), the upper lip 1.5–5.5 mm long; stamens 1.2–6.5 mm long; seeds pubescent or with hairlike papillae (glabrous in *H. peloria*).
8. Leaves up to 13 mm long; corolla 6.5–7.5 mm long, the lower lip 2.5–3.5 mm long; stamens 1.2 mm long with thecae 1 mm long; style 1.8–2.5 mm long; Yucatán Peninsula. *H. websteri*
8. Leaves up to 105 mm long; corolla 8–17 mm long, the lower lip 4–9 mm long; stamens 2.5–6.5 mm long with thecae 1.2–2.6 mm long; style 3.5–9.5 mm long; plants occurring to the west of the Yucatán Peninsula.
9. Bracts 6–13 mm long; bractlets 6–10.5 mm long; corolla pubescent with eglandular trichomes on external surface; seeds glabrous, covered with stout papillae or tubercules.
10. Cauline trichomes to 0.1 mm long; bracts lanceolate, 0.8–1.2 mm wide, long-attenuate and recurved at apex; bractlets and calyx lobes recurved; capsule puberulent; Guerrero. *H. caput-medusae*
10. Cauline trichomes 0.1–1 mm long; bracts ovate-elliptic to obovate, 2.8–5 mm wide, rounded to acute and erect at apex; bractlets and calyx lobes erect; capsule glabrous; Durango and Zacatecas. *H. peloria*
9. Bracts 1.5–6 mm long; bractlets 1.5–4 mm long; corolla pubescent with glandular (sometimes absent in *H. parayana* and *H. pallida*) and eglandular trichomes on external surface; seeds pubescent with dendroid trichomes.
11. Inflorescence axis pubescent with crooked, interwoven, eglandular trichomes obscuring the axis; bracts broadly ovate to orbicular, 1.5–2 mm long. *H. hintonii*
11. Inflorescence axis pubescent with straight to ascendent to recurved to flexuose, eglandular (and often glandular) trichomes, these neither crooked, interwoven, nor obscuring the axis; bracts triangular to subulate to lanceolate to ovate, 2–6 mm long.
12. Bracts attenuate to a point but lacking a distinct mucro at apex; upper

lip of corolla 3–5.5 mm long; staminode 0.6–1.2 mm long; capsule 11–17 mm long.

13. Cauline trichomes ascendent-appressed, 0.1–0.5 mm long; corolla horizontal during anthesis; stamens 3–3.2 mm long with thecae 1.2–1.5 mm long; style 5–6 mm long; seeds 2.5–3 mm long; Chiapas.

..... *H. parayana*

13. Cauline trichomes retrorse, 0.05–0.2 mm long; corolla more or less vertical during anthesis; stamens 5.5–6.5 mm long with thecae 2–2.6 mm long; style 7–9.5 mm long; seeds 4.5–5.5 mm long; Oaxaca.

..... *H. leticihana*

12. Bracts mucronate at apex; upper lip of corolla 1.5–3 mm long; staminode 0.1–0.3 mm long; capsule 7–9 mm long.

14. Bractlets 1–1.5 mm wide; corolla 8–10 mm long, the upper lip 1.5–2 mm long; stamens 2.5–3 mm long; style 3.5–4.5 mm long; capsule glabrous; Jalisco and Colima.

..... *H. anisophylla*

14. Bractlets 0.8–1 mm wide; corolla 10–12 mm long, the upper lip 2–3 mm long; stamens 3.5–4 mm long; style 5.3–6 mm long; capsule pubescent; Sonora and Sinaloa.

..... *H. pallida*

***Holographis tolantongensis* T. F. Daniel, sp. nov.**
(Figures 1, 2)

TYPE.—MEXICO. Hidalgo: Mpio. Cardonal, Barranca de Tolantongo, lado oeste, 45 km NE of Ixmiquilpan, 10 February 1982, R. Hernández M. y P. Tenorio L. 6948 (Holotype: MEXU!; isotype: CAS!).

Suffrutex usque ad 6 dm altus. Caules juniores pubescentes trichomatibus eglandulosis 0.05–0.7 mm longis. Folia opposita petiolata, lamina lanceolata vel ovata vel elliptica 13–32 mm longa 3.5–14 mm lata 2.3–4.7-plo longior quam latior margine revoluta. Inflorescentia spicata, bracteae lanceolatae 6.5–9 mm longae 1.5–2.5 mm latae apice acuminatae erectae, bracteolae lancisubulatae 5.5–7 mm longae 1–1.5 mm latae apice subaristatae erectae. Calyx 7.5–10 mm longus, corolla rosea-purpurea 12–13 mm longa extus glabra, stamina 4.5 mm longa, stylus 7–7.5 mm longus. Capsula ignota.

Subshrub to 6 dm tall. Young stems evenly pubescent with understory of straight to antrorse, eglandular trichomes 0.05–0.2 mm long and sparse overstory of straight to flexuose, eglandular trichomes 0.3–0.7 mm long. Leaves opposite, petiolate, petioles 2–6 mm long, blades coriaceous, lanceolate to ovate to elliptic, 13–32 mm long, 3.5–14 mm wide, 2.3–4.7 times longer than wide, acute at apex, acute at base, adaxial surface dark green, evenly pubescent with flexuose to antrorse-flexuose trichomes to 1 mm long (strigose), abaxial surface light green, pubescent along veins and glabrous or nearly so in inter-

costal regions, margin revolute. Inflorescence of terminal spikes to 3.5 cm long, flowers opposite at nodes, rachis strigose. Bracts lanceolate, 6.5–9 mm long, 1.5–2.5 mm wide, acuminate and erect at apex, abaxial surface strigose. Bractlets lance-subulate, 5.5–7 mm long, 1–1.5 mm wide, shorter than bracts, subaristate and erect at apex, margin often hyaline. Calyx 7.5–10 mm long, lobes narrowly lanceolate to lance-subulate, unequal in length and overlapping one another, sparsely strigose distally, aristate and erect at apex, margins often hyaline. Corolla pinkish-purple, somewhat intermediate between vertical and horizontal during anthesis, 12–13 mm long, glabrous on external surface, tube 7–7.5 mm long, upper lip 4–4.5 mm long with lobes 2–2.5 mm long, lower lip 6–7 mm long with obovate lobes 5–6 mm long. Stamens 4.5 mm long, filaments pubescent, thecae 1.4–1.5 mm long, pollen (observed in Diaphane) prolate, 32–39 μ m long (polar diameter), 25–27 μ m wide (equatorial diameter), 1.3–1.6 times longer than wide, colpi indistinct; staminode 2 mm long, pubescent at apex. Style 7–7.5 mm long, glabrous; stigma asymmetric, 0.2 mm long; ovary glabrous. Capsule unknown.

DISTRIBUTION AND PHENOLOGY.—Known only from the Barranca de Tolantongo in central Hidalgo, Mexico (Fig. 3). The plants occur abundantly in rocky soil with *Pinus pinceana* Gordon, *Quercus opaca* Trel., *Gochnatia hypoleuca* (DC.) A. Gray, and *Juniperus* L. at an elevation of about 2,000 m. Flowering: February.

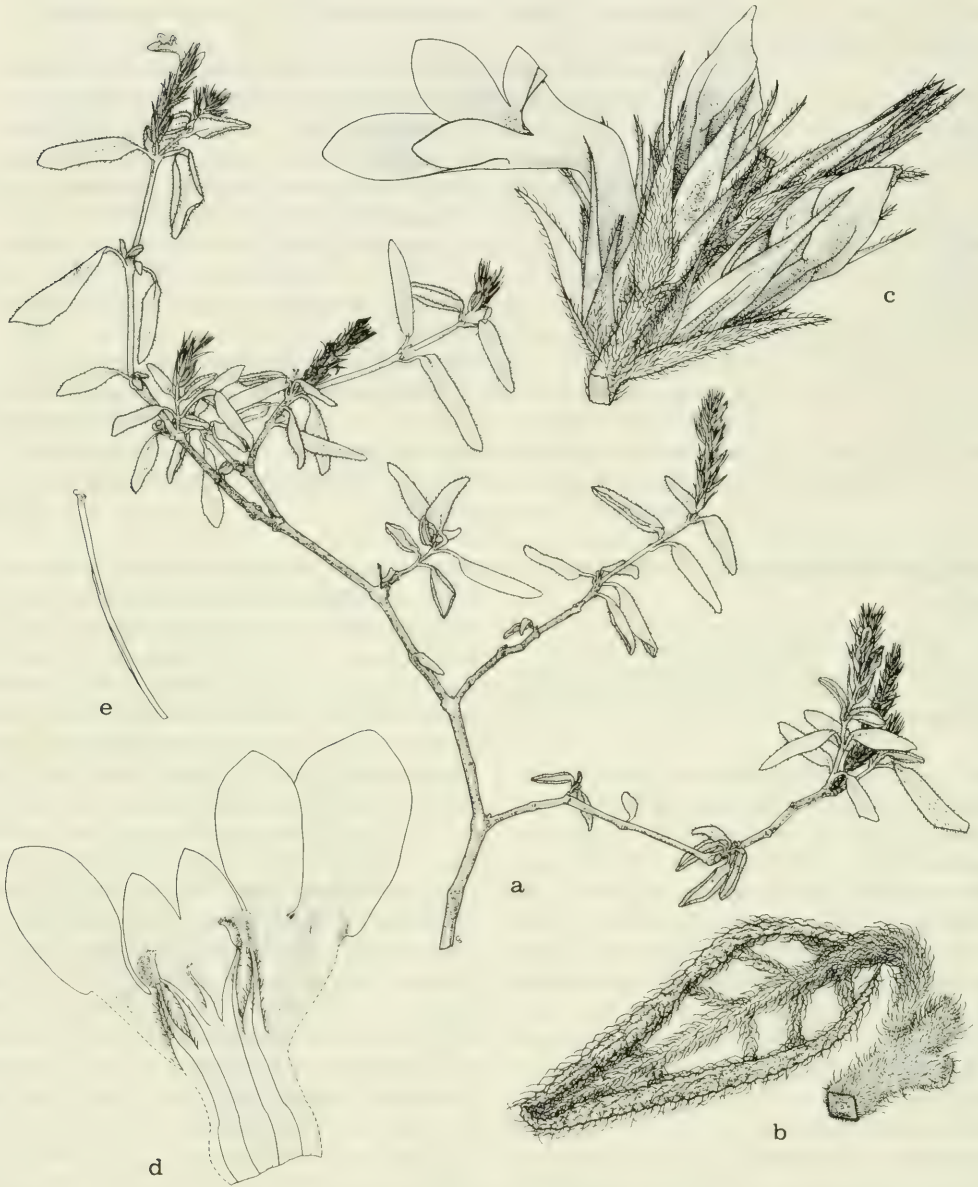


FIGURE 1. *Holographis tolantongensis* (Hernández M. y Tenorio L. 6948). a, Habit, $\times 0.5$; b, Leaf and section of stem, $\times 3.3$; c, Portion of inflorescence, $\times 3.5$; d, Corolla cut open to show androecium, $\times 3.5$; e, Style, $\times 4.6$.

Holographis tolantongensis exhibits the following unique combination of characters: opposite leaves, bracts with the abaxial surface pubescent, pinkish-purple corollas with the external surface glabrous, and calyces 7.5–10 mm long. The only other species of *Holographis* known from Hidalgo, *H. ehrenbergiana*, has mostly whorled leaves and yellow corollas.

***Holographis caput-medusae* T. F. Daniel, sp. nov.**
(Figures 2, 4)

TYPE.—MEXICO. Guerrero: along road from Petatlán to Camalotito, 9.8 km SW of Camalotito, 8 March 1987, T. F. Daniel and B. Bartholomew 4918 (Holotype: CAS!; isotypes: K!, MEXU!, MICH!, NY!, US!).

Herba perennis usque ad 4 dm alta. Caules juniores pubescentes trichomatibus inconspicuis

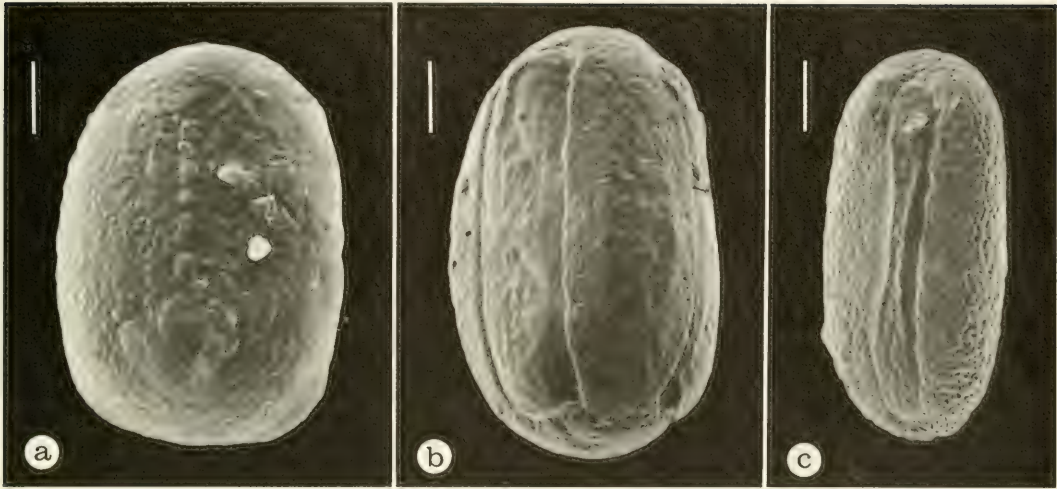


FIGURE 2. Scanning electron micrographs of pollen of *Holographis*. a, *H. tolantongensis* (Hernández M. and Tenorio L. 6948), scale equals 6 μ m; b, *H. caput-medusae* (Daniel and Bartholomew 4918), scale equals 6 μ m; c, *Holographis leticiiana* (Torres C. et al. 637), scale equals 7.5 μ m.

retrorsi eglandulosi usque ad 0.1 mm longis. Folia verticillata in quoque nodo quatuor sessilia vel subsessilia, lamina anguste elliptica vel elliptica vel ovato-elliptica vel obovato-elliptica 30–97 mm longa 10–40 mm lata 2.1–6-plo longior quam latior margine plana. Inflorescentia spicata, bracteae lanceolatae 6–8 mm longae 0.8–1.2 mm latae apice longiattenuatae recurvatae, bracteolae lanceolatae 6–8 mm longae 0.5–1 mm latae apice longiattenuatae recurvatae. Calyx 8.5–10 mm longus, corolla albida et rosea 11–14 mm

longa extus pubescens, stamina 3.5 mm longa, stylus 6.5–7.5 mm longus. Capsula 8–9 mm longa puberula. Semina 2.2–3 mm longa, 1.8–2 mm lata.

Perennial herb to 4 dm tall. Young stems inconspicuously pubescent with retrorse, eglandular trichomes up to 0.1 mm long concentrated in two vertical lines to glabrous. Leaves whorled (four/node), sessile to subsessile, petioles (if present) up to 1 mm long, blades chartaceous, narrowly elliptic to elliptic to ovate-elliptic to ob-

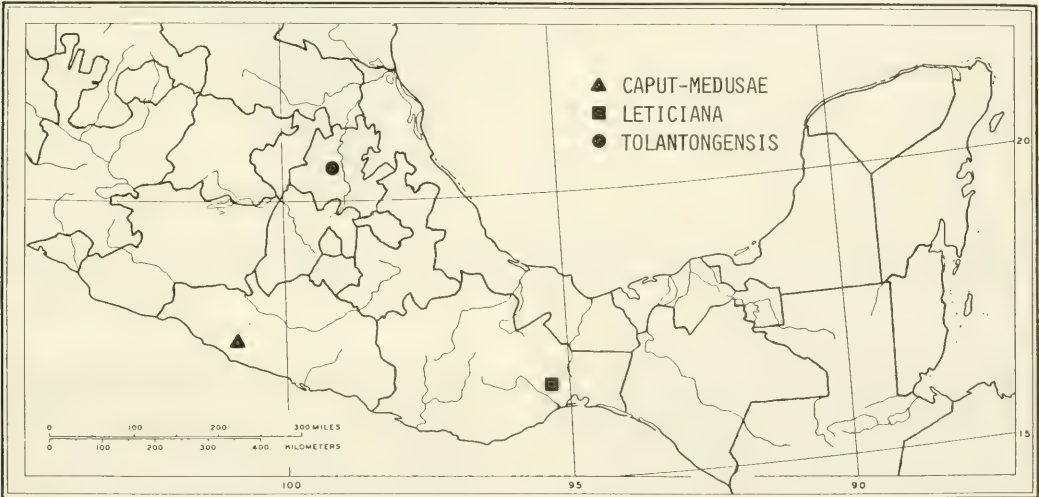


FIGURE 3. Map showing distribution of *Holographis caput-medusae*, *H. leticiiana*, and *H. tolantongensis*.



FIGURE 4. *Holographis caput-medusae* (Daniel and Bartholomew 4918). a, Habit, $\times 0.5$; b, Inflorescence, $\times 3.4$; c, Corolla, $\times 3.6$; d, Corolla cut open to show androecium, $\times 4.3$; e, Capsule, $\times 4$; f, Seed, $\times 11.5$.

ovate-elliptic, 30–97 mm long, 10–40 mm wide, 2.1–6 times longer than wide, acuminate at apex, attenuate nearly to or to the node at base, adaxial surface sparsely pubescent with coarse, antrorse, eglandular trichomes 0.2–0.5 mm long, abaxial surface glabrous or nearly so, margin entire to somewhat undulate, flat. Inflorescence of axillary

spikes to 3 cm long, flowers opposite at nodes, rachis evenly and densely pubescent with straight, eglandular trichomes to 0.05 mm long. Bracts lanceolate, 6–8 mm long, 0.8–1.2 mm wide, abaxial surface pubescent like rachis, apex long-attenuate and recurved. Bractlets lanceolate, 6–8 mm long, 0.5–1 mm wide, approximately equal

in length to bracts, pubescent like bracts, apex long-attenuate and recurved. Calyx 8.5–10 mm long, lobes equal in length and slightly overlapping one another, pubescent like bracts, long-attenuate and recurved at apex, margin hyaline proximally. Corolla whitish with pink lines on lower lip, horizontal during anthesis, 11–14 mm long, pubescent on external surface with eglandular trichomes 0.05–0.1 mm long, tube 5–7 mm long, upper lip 4.5–5.5 mm long with linear-elliptic lobes 4.5–5.5 mm long, lower lip 6–7 mm long with elliptic to obovate lobes 3–4.7 mm long. Stamens 3.5 mm long, filaments pubescent, thecae 1.3–1.6 mm long, pollen (observed in *Diaphane*) prolate, 34–42 μ m long (polar diameter), 25–27 μ m wide (equatorial diameter), 1.4–1.6 times longer than wide, colpi distinct; staminode 0.6 mm long, pubescent at apex. Style 6.5–7.5 mm long, sparsely pubescent; stigma unequally bilobed, 0.2–0.3 mm long. Capsule 8–9 mm long, puberulent with trichomes less than 0.05 mm long. Seeds subelliptical to subrectangular in outline, 2.2–3 mm long, 1.8–2 mm wide, surfaces covered with hairlike papillae to 0.1 mm long.

DISTRIBUTION AND PHENOLOGY.—Known only from the seaward slopes of the Sierra Madre Sur in western Guerrero (Fig. 3) in a region of tropical dry forest at an elevation of approximately 150 m. Flowering and fruiting: March.

Holographis caput-medusae is unique in the genus by virtue of its relatively long, attenuate-recurved bracts, bractlets, and calyx lobes. These give the dense spikes a medusoid appearance. *Holographis caput-medusae* is the third species of the genus to be found in Guerrero. Unlike the other two, *H. argyrea* and *H. hintonii*, it occurs in the Pacific lowlands. The holotype was collected in a weedy thicket rich in Acanthaceae, including: *Aphelandra scabra* (Vahl) Smith, *Carlownrightia arizonica* A. Gray, *Dicliptera resupinata* (Vahl) Juss., *Elytraria imbricata* (Vahl) Pers., *Henrya insularis* Nees, *Odontonema auriculatum* (Rose) T. Daniel, *Ruellia albiflora* Fernald, *Tetramerium nervosum* Nees, and *Tetramerium tenuissimum* Rose.

***Holographis leticiana* T. F. Daniel, sp. nov.**

(Figures 2, 5)

TYPE.—MEXICO. Oaxaca: Distr. Tehuantepec, subida al Cerro Guiengola por la ladera S donde está la fábrica de cal, 25 October 1986, M. Leticia Torres C., R. Torres C., y C. Martínez 637 (Holotype: MEXU!; isotypes: CAS!, and others to be distributed).

Frutex usque ad 1 m altus. Caules juniores puberuli trichomatibus glandulosis 0.05–0.2 mm longis. Folia verticillata in quoque nodo quatuor petiolata, lamina ovata vel ovato-elliptica 17–82 mm longa 9–27 mm lata 1.5–3-plo longior quam latior margine plana. Inflorescentia spicata, bractae lanceolatae vellanci-subulatae 2.5–4 mm longae 0.9–1.1 mm latae apice attenuatae erectae, bracteolae subulatae 2.3–3.5 mm longae 0.5–0.7 mm latae apice attenuatae erectae. Calyx 4–5 mm longus, corolla rosea 9.5–14.5 mm longa extus pubescens, staminia 5.5–6.5 mm longa, stylus 7–9.5 mm longus. Capsula 11–17 mm longa glabra. Semina 5–5.5 mm longa, 3.8–4.5 mm lata.

Shrub to 2 m tall. Young stems evenly puberulent with retrorse, eglandular trichomes 0.05–0.2 mm long. Leaves whorled (four/node), petiolate, petioles 2–17 mm long, blades chartaceous, ovate to ovate-elliptic, 6–90 mm long, 4–42 mm wide, 1.5–3 times longer than wide, acute to acuminate at apex, acute to attenuate at base, surfaces pubescent with straight to subflexuose to antrorse, eglandular trichomes to 0.2 mm long, margin entire to subundulate, flat. Inflorescence of axillary spikes to 2.5 cm long, flowers opposite at nodes, rachis evenly and densely pubescent with erect to downward pointing, eglandular trichomes 0.1–0.2 mm long. Bracts lanceolate to lance-subulate, 2–4 mm long, 0.9–1.1 mm wide, abaxial surface pubescent with erect to subflexuose or downward pointing, eglandular trichomes to 0.2 mm long, apex attenuate, erect. Bractlets subulate, 2–3.5 mm long, 0.5–0.7 mm wide, shorter than or equal to bracts, pubescent like bracts, apex attenuate, erect. Calyx 3–5 mm long, lobes equal in length and slightly overlapping one another, lanceolate, pubescent like bracts, attenuate and erect at apex. Corolla greenish-white with pinkish or maroon stripes on lower lip, more or less vertical during anthesis, 9.5–14.5 mm long, pubescent on external surface with glandular and eglandular trichomes 0.05–0.2 mm long, tube 2.5–5 mm long, abruptly expanded into a throat 2.5–3.5 mm long, upper lip 3–5.5 mm long with triangular lobes 1–1.5 mm long, lower lip 4.5–7 mm long with obovate lobes 2.5–5 mm long. Stamens 5.5–6.5 mm long, filaments pubescent, thecae 2–2.6 mm long, pollen (observed in *Diaphane*) prolate, 32–39 μ m long (polar diameter), 22–25 μ m wide (equatorial diameter), 1.3–1.8 times longer than wide, colpi distinct; staminode 0.7–1.2 mm long, sparsely

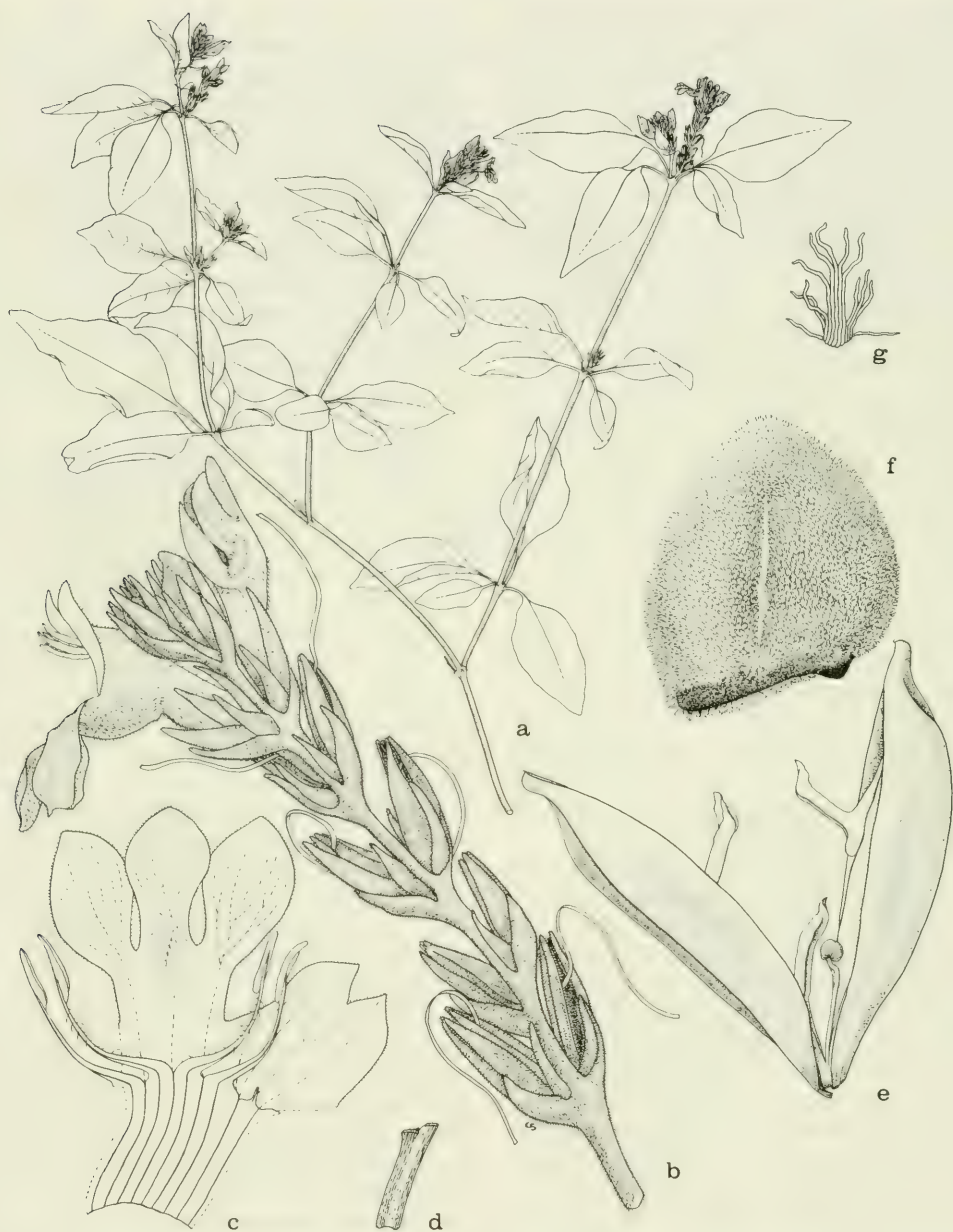


FIGURE 5. *Holographis leticiana*. a, Habit (Daniel 5386), $\times 0.5$; b, Inflorescence (Daniel 5386), $\times 4$; c, Corolla cut open to show androecium (Torres C. 637), $\times 4$; d, Distal portion of style and stigma (Daniel 5386), $\times 16$; e, Capsule (Torres C. 773), $\times 3.4$; f, Seed (Torres C. 773), $\times 8$; g, Seminal trichome (Torres C. 773), $\times 42$.

pubescent at apex. Style 7–9.5 mm long, very sparsely pubescent to glabrous; stigma indistinctly bilobed, 0.1 mm long. Capsule 11–18 mm long, glabrous. Seeds subrectangular to subelliptical in outline, 4.5–5.5 mm long, 3.5–4.5 mm

wide, surfaces covered with golden to brown, dendritic trichomes to 0.4 mm long.

DISTRIBUTION AND PHENOLOGY.—Known only from the vicinity of the Cerro Guiengola in southeastern Oaxaca (Fig. 3), where the plants

occur in tropical deciduous forest dominated by legumes and cereoid cacti at elevations from 60 to 600 m. Flowering and fruiting: October–March.

Holographis leticiana can be distinguished from all other species in the genus by the following combination of characters: whorled leaves, pinkish corollas, and stamens 5.5–6.5 mm long. It is most similar to *H. parayana*, a species occurring approximately 200 km to the east in Chiapas. The contrasting features of these two species are summarized in the key above. Plants of this species collected in November 1987 (*Daniel 5386*) were locally common understory shrubs. Flowers were visited by both bombyliid flies and megachilid bees. However, pollen similar to that of *Holographis* was not located on individuals of either. Other Acanthaceae growing with *H. leticiana* include *Tetramerium oaxacanum* T. Daniel and species of *Ruellia* L. and *Siphonoglossa* Oersted.

PARATYPES.—MEXICO. Oaxaca: along road to Ruinas Guiengola, 1.3–1.6 km N of Mex. 190 between Jalapa de Marques and Tehuantepec, *T. Daniel 5386* (CAS, DUKE, F, GH, K, MICH, MEXU, MO, NY, TEX, US); 61.8 km NW of Tehuantepec, *P. Fryxell and E. Lott 3403* (CAS); Distr. Tehuantepec, Ruinas del Cerro Guiengola, *M. L. Torres C. et al. 511* (CAS, MEXU); Distr. Tehuantepec, ladera S del Cerro Guiengola por la fábrica de cal, *M. L. Torres C. et al. 773* (CAS, MEXU); Distr. Tehuantepec, hacia el N a 300 m del

“Mango,” por la subida al Ocotil Cerro Guiengola, *M. L. Torres C. et al. 834* (CAS, MEXU).

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THE EELPOUT GENUS *PACHYCARA* (TELEOSTEI: ZOARCIDAE)
IN THE NORTHEASTERN PACIFIC OCEAN, WITH
DESCRIPTIONS OF TWO NEW SPECIES

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ABSTRACT: The eelpout genus *Pachycara* Zugmayer, 1911, is recognized from the North Pacific Ocean for the first time. Four species are included, two of which—*P. gymninium* and *P. lepinium*—are new. *Pachycara gymninium* differs from *P. lepinium* mainly in having a scaleless nape, the mediolateral lateral line originating in the pectoral axil versus posterior to the pectoral margin, more numerous precaudal vertebrae, and shorter pectoral and pelvic fins. The type species of *Pachycara*—*P. obesum*—from the abyssal Atlantic, is shown to be synonymous with the earlier described *Maynea bulbiceps* Garman, 1899, from the eastern tropical Pacific. Another species described by Garman (1899)—*Phucocoetes suspectus*—is placed in *Pachycara* and redescribed from three specimens.

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INTRODUCTION

The eelpout genus *Pachycara* was erected for a single specimen taken in the Bay of Biscay at a depth of 4,780 m by the expeditions of Prince Albert I of Monaco (Zugmayer 1911a, b). A second (juvenile) specimen of the type species, *P. obesum*, was described from off Virginia by Markle and Sedberry (1978). Earlier, Garman (1899) described *Maynea bulbiceps* from the eastern tropical Pacific (Gulf of Panama). This species was placed in *Pachycara* as a putative Pacific sister species of *P. obesum* by Anderson (1984).

Anderson (1988) included an Antarctic species, first described as *Lycodes brachycephalus* by Pappenheim (1912), in *Pachycara* because it lacked the three apomorphic characters previously established for *Lycodes* (Anderson 1984): 1) possession of cartilaginous laminae along the ventral surface of the dentary bones ("mental crests" of Andriashev 1954); 2) loss of the palatine membrane (oral valve); and 3) loss of head pores in adults (except for some pedomorphic species). Anderson (1984) included 11 species in *Pachycara*, only three of which had been de-



FIGURE 1. *Pachycara bulbiceps* (Garman), BCPM 980-99, 525 mm SL, off the Queen Charlotte Islands, British Columbia.

scribed previously, and a revision of the genus is in progress.

The purpose of this paper is to describe in advance of the senior author's revision two new species of *Pachycara* from the northeastern Pacific Ocean that have been known in collections for many years. In addition, we redescribe the type species, *P. obesum*, herein synonymized with *P. bulbiceps*, now known from six North Atlantic and 32 northeastern Pacific specimens, as well as the rare *P. suspectum*, known from three specimens.

METHODS

Measurements were made with an ocular micrometer or dial calipers to the nearest 0.1 mm. Definitions of characters and methodology follows Gosztonyi (1977), or, in cases of contradiction, Peden and Anderson (1978) and Anderson (1982, 1984). All specimens were measured and radiographed to create Table 1, except 16 of 38 *P. gymninium* in SIO 67-121. Character state modifiers are based on those numerically scored characters of Anderson (1984). Museum abbreviations follow Leviton et al. (1985). Measurements are in standard length (SL). Certain proportions expressed in percent head length (HL) or SL.

KEY TO NORTHEASTERN PACIFIC *PACHYCARA* SPECIES

- 1A. Pelvic fins present 2
- 1B. Pelvic fins absent
..... *Pachycara bulbiceps* (Garman, 1899)
- 2A. Number of precaudal vertebrae 21-23;
lateral line with complete, ventral branch
only; head length 15.6-17.7% SL; anal fin
origin associated with vertebrae 20-22 ...
..... *Pachycara suspectum* (Garman, 1899)
- 2B. Number of precaudal vertebrae 23-31
(usually 25 or more); lateral line with
complete mediolateral and ventral
branches; head length 12.0-15.9% SL;

anal fin origin associated with vertebrae
23-31 3

- 3A. Scales present on nape; mediolateral
branch of lateral line originating posterior
to pectoral fin margin; pectoral fin length
72.5-89.9% HL; pelvic fin length 11.5-
17.3% HL; number of precaudal verte-
brae 23-26 *Pachycara lepinium* n. sp.
- 3B. Scales absent on nape (rarely present in
small patches immediately anterior to
dorsal fin origin); mediolateral branch of
lateral line originating in pectoral axil;
pectoral fin length 63.0-70.8% HL; pelvic
fin length 4.8-11.3% HL; number of pre-
caudal vertebrae 28-31
..... *Pachycara gymninium* n. sp.

Pachycara bulbiceps (Garman, 1899)

(Figures 1-3)

- Maynea bulbiceps* Garman, 1899:140, 141, pl. E, fig. 1.
McAllister and Rees 1964:106, 107. Percy et al. 1982:387,
399, 400.
Pachycara obesa Zugmayer, 1911a:12; 1911b:134-136, pl. VI,
fig. 6. Markle and Sedberry 1978:22-25, fig. 1. Merrett and
Marshall 1981:240. Andriashev 1973:547.
Pachychara obesa Zugmayer (lapsus calami). Fowler 1936:
1056, fig. 47. Andriashev 1986:1149, text fig.

MATERIAL EXAMINED.—Northeastern Atlantic: MOM, uncat. (holotype of *Pachycara obesa*); Bay of Biscay; 45°27'N, 06°05'W; 4,780 m; PRINCESSE ALICE sta. 1554; 7-9 Sept. 1903. BMNH 1981.6.16:15 (1); off Cap Blanc, West Africa; 20°17.2'N, 21°42.3'W; 4,002-4,007 m; DISCOVERY sta. 9131; 17 Nov. 1976. IOS, uncat. (1); off Senegal; 18°08.6'N, 20°11.7'W; 3,120 m; DISCOVERY sta. 10884; 12 Aug. 1983. IOS, uncat. (1); Porcupine Sea Bight; 49°37.1'N, 13°48.5'W; 3,990-3,920 m; DISCOVERY sta. 51803; 26 Sept. 1983. Northwestern Atlantic: USNM 215611 (1); off Virginia; 36°42.0'N, 74°04.5'W; 2,400-2,450 m; EASTWARD cr. 7506, sta. 20; 24-25 July 1975. MCZ 57612 (1); Middle Atlantic Bight; 38°44.0'N, 70°10.0'W; 3,028 m; OCEANUS cr. 93, sta. 911; 31 Mar. 1981. Gulf of Panama: MCZ 28681 (holotype of *Maynea bulbiceps*); 06°10'N, 83°06'W; 2,690 m; ALBATROSS sta. 3361; 25 Feb. 1890. UMML 22860 (2); 06°53-49'N, 79°27-28'W; 3,193-3,201 m; JOHN E. PILLSBURY sta. P-526; 5 May 1967. UMML 33484 (1); 06°47-48'N, 79°13'-80°00'W; 3,045-3,218 m; JAMES M. GILLISS sta. GS-3; 14 Jan. 1972. UMML 33485 (2); 06°52'N, 79°28'W; 3,200-3,229 m; JAMES M. GILLISS sta. GS-1; 13-14 Jan. 1972. SIO 81-148 (4); 05°09.8'N,

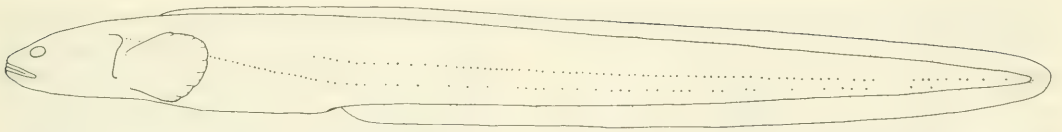


FIGURE 2. *Pachycara bulbiceps* (Garman), diagrammatic of CAS 55588, 338 mm SL, from the Gulf of Panama, showing extent of lateral lines.

81°41.2'W; 3,900–4,000 m; MELVILLE; 3 Oct. 1981. SIO 85-33 (4); 05°20.6'N, 81°55.5'W; 3,866 m; DSRV ALVIN dives 1361, 1363; 9–12 Apr. 1984. CAS 55588 (1); recat. from SIO 81-148. Middle American Trench: SIO 73-286 (3); off Costa Rica; 09°43.8'N, 86°02.0'W; 2,601 m; ALEXANDER AGASSIZ; 19–20 Apr. 1973. SIO 73-268 (1); off Guatemala; 13°27.0'N, 91°59.2'W; 3,332 m; ALEXANDER AGASSIZ; 13–14 Apr. 1973. Mexico: SIO 66-35 (1); off Guadalupe Isl.; 29°01.0'N, 118°01.2'W; 3,310 m; ALEXANDER AGASSIZ; 5–6 Apr. 1966. Cascadia Abyssal Plain (off Oregon): OSUO 2559 (2); 45°27.8–27.0'N, 126°17.4–21.0'W; 2,606 m; YAQUINA sta. CP-2C, BMT 157; 17 Jan. 1970. OSUO 2560 (2); 46°02.2'N, 126°33.5–28.5'W; 2,706 m; YAQUINA sta. CP-2A, BMT 257; 15 Feb. 1971. OSUO 2561 (2); 45°18.0–17.0'N, 126°26.4–30.5'W; 2,710 m; YAQUINA sta. CP-2C, BMT 266; 18 Feb.

1971. OSUO 2562 (1); 44°43.1–46.0'N, 127°29.3–28.6'W; 2,818 m; YAQUINA sta. CP-3E, BMT 317; 3 Feb. 1973. CAS 61220 (2); 44°39.7–39.0'N, 126°39.6–44.8'W; 2,816 m; CAYUSE sta. CP-2E, BMT 253; 30 Sept. 1970. LACM 44316-1 (1); 45°20.6–20.9'N, 126°35.7–39.7'W; 2,750 m; YAQUINA sta. CP-2C, BMT 264; 17 Feb. 1971. LACM 44317-1 (1); 46°01.4–05.0'N, 127°31.0–32.5'W; 2,835 m; YAQUINA sta. CP-3A, BMT 322; 12 Mar. 1973. British Columbia: BCPM 980-99 (1); off Queen Charlotte Isl., W of Tasu Sound; 2,780 m; EASTWARD HO set 17; 26 Aug. 1979.

DIAGNOSIS.—A species of *Pachycara* as defined by Anderson (1984) distinguished by the following combination of characters: pelvic fins



FIGURE 3. Group of *Pachycara* sp. (presumably *P. bulbiceps*) near a baitfall in the Gulf of Panama (05°20'N, 81°55'W; depth, 3,850 m). Photographed by Craig R. Smith, University of Washington, DSRV ALVIN dive 1140, 28 Sept. 1981.

TABLE 1. COUNTS AND MEASUREMENTS OF NORTHEASTERN PACIFIC *PACHYCARA* SPECIES, INCLUDING ATLANTIC MATERIAL OF *P. BULBICEPS*.

	<i>P. bulbiceps</i> (Atlantic)	<i>P. bulbiceps</i> (Pacific)	<i>P. gymninium</i>	<i>P. lepinium</i>	<i>P. suspectum</i>
Measurements, in percent SL					
Head length	12.3–15.0	11.8–14.8	12.0–15.6	13.8–15.9	15.6–17.7
Head width	5.7–8.5	5.5–10.1	5.7–8.2	6.5–11.8	8.0–8.9
Pectoral length	9.9–12.2	8.7–12.9	8.3–10.3	10.2–13.5	9.1–10.1
Predorsal length	17.8–18.7	16.0–19.8	15.9–21.5	15.8–23.2	15.9–18.2
Prenal length	34.9–40.1	35.1–40.0	38.5–44.1	34.3–41.9	35.8–36.0
Body height	6.4–12.7	5.7–11.6	7.4–13.6	8.3–16.9	8.4–9.9
Gill slit length	4.9–5.9	4.1–6.9	3.3–5.2	4.9–9.4	7.0 (in 1)
Caudal fin length	2.4–4.2	1.5–3.6	1.9–5.2	1.5–2.7	3.2 (in 1)
Measurements, in percent HL					
Head width	38.8–73.1	43.5–80.5	37.3–64.1	44.5–75.3	49.7–52.7
Upper jaw length	33.9–43.2	37.1–52.7	33.3–52.8	35.9–52.0	38.4–41.4
Pectoral length	67.8–99.5	64.1–99.9	63.0–70.8	72.5–89.9	57.4–58.6
Snout length	19.4–22.7	16.8–26.2	15.8–25.5	17.6–25.9	18.5–22.3
Eye diameter	16.2–26.4	11.5–22.4	13.6–23.3	12.4–18.7	16.8–19.5
Gill slit length	32.9–50.9	31.4–49.8	21.0–43.1	33.9–59.8	39.7 (in 1)
Interorbital width	10.6–17.4	7.0–11.5	9.1–11.3	7.1–13.8	6.4–7.3
Interpupillary width	26.4–38.0	18.2–32.8	26.9–35.7	22.3–44.4	24.2 (in 1)
Pelvic fin length	absent	absent	4.8–11.3	11.5–17.3	9.7–11.7
Counts					
Vertebrae	25–31 + 82–90 = 113–118	27–31 + 83–91 = 112–119	28–31 + 73–80 = 102–109	23–26 + 80–94 = 105–120	21–23 + 84–87 = 105–110
Dorsal fin rays	104–109	105–114	96–103	99–113	100–106
Anal fin rays	86–94	88–97	77–84	85–98	85–89
Caudal fin rays	8–12	10–12	10–12	9–12	9
Pectoral fin rays	16–19	16–18	14–18	15–18	16
Pelvic fin rays	absent	absent	3	3	3
Gill rakers	2–3 + 11–13 = 13–16	0–4 + 11–15 = 11–19	3–5 + 10–14 = 13–19	2–5 + 11–15 = 12–19	1–2 + 14–15 = 16
Vomerine teeth	3–6	2–9	3–8	5–18	3–6
Palatine teeth	2–7	4–10	3–14	7–40	9–12

absent; mediolateral branch of lateral line originating posterior to pectoral fin margin; scales absent on nape; vertebrae 25–31 + 82–91 = 112–119; head length 11.8–15.0% SL; anal fin origin associated with vertebrae 23–30.

DESCRIPTION.—Counts and measurements presented in Table 1 were compiled from all known specimens, 82–525 mm SL (no gravid females). The following description is based on 10 adult males, eight adult females, 10 juveniles of both sexes, and seven eviscerated specimens. Head large, ovoid, wider in adults than juveniles. Smallest specimen (82 mm SL) with most dorsoventrally depressed head, resulting in more acute snout than adults. Body short, deep, broader in cross section in adults than juveniles. Body more slender than similarly sized *P. gymninium*

and *P. lepinium*; body height at anal fin origin of smallest specimen (5.7% SL; Table 1) measuring like slender genus *Lycenchelys*, however specimens >160 mm with body height $\geq 7.8\%$ SL. Tail laterally compressed, more so posteriorly, tapering gradually to tip. Skin firm, not gelatinous, but pliable around head, especially near mouth, cheeks, and nape due to subdermal lipid layer. Scales minute, cycloid, imbedded, covering body, tail, and vertical fins to one-half to three-fourths their height; no scales on head or nape; scales present on pectoral axil and base, and on breast to isthmus in largest specimens. No scales developed in smallest specimen. Eye circular, larger in proportion to head in smallest specimens than largest adults. Gill slit short, usually extending ventrally to lower margin of pec-

toral base. Very slight, squared-off lobe formed at dorsal margin of operculum, this best developed in small juveniles; gill slit of large adults often without distinct lobe. Single pair of nostrils at snout tip, nasal tube not reaching upper lip. Pectoral fin large, its origin at or just below body midline; posterior margin somewhat wedge-shaped to almost evenly rounded; lowermost 6–9 rays shorter and thicker than others, their tips not at all or slightly exserted; pectoral rays usually 17–18 (Table 2).

Mouth terminal, upper jaw slightly longer in relation to head in adult males than comparably sized females; upper jaw 45.0–52.7% HL ($\bar{x}$ = 48.8%, n = 10) in males over 330 mm SL, 41.8–44.6% HL ($\bar{x}$ = 43.1%, n = 5) in females over 330 mm SL. Minute epidermal prickles on lips and occasionally in patches on snout. Palatine membrane (oral valve) moderately developed in adults, not reaching vomer, larger in juveniles, reaching anterior edge of vomer. Teeth in jaws and palate small, conical, dentition not sexually dimorphic. Jaw teeth in single row in smallest specimen; premaxillae of adults with 2–3 rows anteriorly, blending into single, posterior row; dentary with 3–5 rows anteriorly, blending into single or double posterior row. Vomerine teeth in irregular patch; palatine teeth in single row.

Cephalic lateralis system reduced, numerical variation in pores of postorbital and suborbital canals only. Postorbital pores one, three and four present on one side, pore one only on the other in one specimen; pores one and four present in 21 specimens. Two pairs of anterior supraorbital (nasal) pores, one set mesial to nasal tube, the other posteromesially. Usually six suborbital pores, all emanating from ventral ramus of suborbital bone chain, but a seventh pore emanating from ascending ramus behind eye, just below first postorbital pore on one side in one specimen. Eight (not seven as reported by Markle and Sedberry 1978) preoperculomandibular pores, four emanating from dentary, one from anguloarticular, and three from preopercle. Interorbital and occipital (supratemporal) pores absent. Body lateral line of two branches: mediolateral, originating at or just posterior to pectoral fin margin, complete to tail tip (not evident in some material), and ventral, originating just posterior to fourth postorbital pore, coursing gradually across body to just above anus, then running just above anal fin to tail tip (Fig. 2).

TABLE 2. PECTORAL FIN RAY COUNTS OF NORTHEASTERN PACIFIC *PACHYCARA* SPECIES.

Species	Fin ray number					
	14	15	16	17	18	19
<i>P. gymninium</i> , n = 30	3	12	11	3	1	0
<i>P. lepinium</i> , n = 30	0	1	3	20	6	0
<i>P. bulbiceps</i> , n = 34	0	0	4	20	9	1*
<i>P. suspectus</i> , n = 3	0	0	3	0	0	0

* USNM 215611, recounted after Markle and Sedberry (1978) who reported it as 17.

Vertebrae symmetrical, no geographical variation exhibited numerically. Caudal fin rays variable, with two epural, 4–6 upper hypural, and 3–5 lower hypural rays. Last anal ray associated with second preural vertebra, last dorsal ray associated with third or fourth preural. Dorsal fin origin associated with vertebrae 4–7, with no free pterygiophores. All dorsal elements soft rays, first one not segmented, but bilaterally divided at least near base. Anal fin origin associated with antepenultimate to ultimate precaudal vertebrae, with 3–9 anal fin pterygiophores inserted anterior to haemal spine of first caudal vertebra.

Gill rakers short, roughly triangular in adults, more slender and longer in juveniles; adults with 3–4 epibranchial rakers and usually 12–14 on ceratobranchial; raker denticles absent. Branchiostegal rays six: four articulating with ceratohyal and two with epihyal. Two nublike pyloric caeca, not longer in smallest specimens than largest, as in some zoarcids. Pseudobranch filaments relatively long, about one eye diameter in length in adults (less in smallest specimens), numbering 3–7.

Fresh specimens uniformly dark brown, head and most of pectoral fins darker, but not black. Pectoral base pale in some preserved specimens, with irregular gray mottling in IOS DISCOVERY sta. 51803. Dorsal fin of this juvenile and a large adult (IOS DISCOVERY sta. 10884) with thin white bands over black background mostly at mid-body and near tail tip; anal fin with fewer white bands. Orobranchial chamber pale to dark brown. Abdomen and eyes dark blue in freshly preserved specimens.

DISTRIBUTION.—Presently known from both sides of the North Atlantic at depths of 2,400–4,780 m, and off the Queen Charlotte Islands, British Columbia, to the Gulf of Panama, North Pacific, at depths of 2,601–4,000 m over brown

and green mud bottoms, where the species may swarm near food falls or baited traps (Fig. 3).

***Pachycara suspectum* (Garman, 1899)**

(Figure 4)

Phucocoetes suspectus Garman, 1899:137, pl. XXX, fig. 3, 3a.

MATERIAL EXAMINED.—MCZ 28683 (holotype); off Acapulco, Mexico; 16°33.0'N, 99°52.5'W; 1,207 m; ALBATROSS sta. 3418; 11 Apr. 1890. SIO 68-106 (1); Gulf of California; 25°56.6'N, 110°37.5'W; 1,280 m; 22 Jan. 1968. ZMUC P-761085 (1); Gulf of Panama; 07°22'N, 79°32'W; 915–975 m; GALATHEA sta. 739; 15 May 1952.

DIAGNOSIS.—A species of *Pachycara* as defined by Anderson (1984) distinguished by the following combination of characters: pelvic fins present; lateral line with ventral branch only; scales absent on nape; vertebrae 21–23 + 84–87 = 105–110; head length 15.6–17.7% SL; anal fin origin associated with vertebrae 20–22.

DESCRIPTION.—Counts and measurements presented in Table 1 were compiled from all three specimens (females), 218–280 mm SL; holotype badly damaged. Head large, ovoid, deepest at occiput, dorsoventrally depressed. Snout acute, steeply sloping anteriorly. Body short, deep, ovoid in cross section. Skin firm, not gelatinous, but pliable around mouth and cheeks due to subdermal lipid layer. Scales minute, cycloid, imbedded, sparse anteriorly, covering body and tail, absent on unpaired fins, head, nape, and pectoral base. Eye ovoid, entering dorsal profile of head when viewed laterally. Gill slit long, extending ventrally to near pelvic base. Slight, squared-off lobe formed at dorsal margin of operculum. Single pair of nostrils at snout tip, nasal tube not reaching upper lip. Pectoral fin large, its origin well below body midline; posterior margin wedge-shaped; lowermost 6–7 rays shorter and thicker than others, their tips very slightly exerted.

Mouth terminal, upper jaw extending posteriorly to vertical through middle of eye. No epidermal prickles on lips or snout. Palatine membrane (oral valve) moderately developed, reaching anterior margin of vomer. Teeth in jaws and palate small, conical. Jaw teeth in two rows anteriorly, blending into single posterior row in all three specimens. Vomerine teeth in irregular patch; palatine teeth in single or double (ZMUC P-761085) row.

Cephalic lateralis system reduced, numerical variation not detected (two specimens damaged).

Postorbital pores one, three, and four present in SIO 68-106. Two pairs of anterior supraorbital (nasal) pores, one set mesial to nasal tube, the other dorsally. Seven suborbital bones present from which emanate six pores from ventral ramus of chain and one from ascending ramus behind eye, just below first postorbital pore. Eight preoperculomandibular pores, four emanating from dentary, one from anguloarticular, and three from preopercle. Interorbital and occipital pores absent. Body lateral line of single, complete, ventral branch only; lateral line originating just posterior to fourth postorbital pore, coursing steeply downward on anterior portion of abdomen, then running just above anal fin to tail tip (Garman 1899, pl. XXX).

Vertebrae symmetrical. Caudal fin with one epural and four upper and lower hypural rays (in two). Last anal ray associated with second preural vertebra, last dorsal ray associated with fourth preural vertebrae. Dorsal fin origin associated with vertebrae 2–3, with no free pterygiophores. All dorsal elements soft rays, first one not segmented, but bilaterally divided. Anal fin origin associated with penultimate precaudal vertebra, with 2–4 anal fin pterygiophores inserted anterior to haemal spine of first caudal vertebra.

Gill rakers short, roughly triangular, ventralmost blunt, but dorsalmost 5–6 with sharp tips; raker denticles absent. Branchiostegal rays six: four articulating with ceratohyal and two with epihyal. Two nublike pyloric caeca. Pseudo-branch filaments short, numbering 3–4.

Coloration of fresh specimens not confirmed, although Garman (1899) reported holotype as “blackish.” Recent material greatly faded. One gravid female, 218 mm SL (SIO 68-106), with ova averaging 4.4 mm in diameter.

DISTRIBUTION.—Currently known from the Gulf of California south to the Gulf of Panama at depths of 915–1,280 m over green and brown mud bottoms.

***Pachycara gymninium* n. sp.**

(Figure 5)

Lycodes sp. Hubbs et al., 1979:14.

Lycenchelys “E.” Percy et al., 1982:387.

HOLOTYPE.—USNM 280121 (female, 422 mm SL); British Columbia, W of Tasu Sound, Queen Charlotte Islands; 52°38.0'N, 132°05.8'W; trap, 2,744 m; TALAPUS set 18; 4 Feb. 1980.

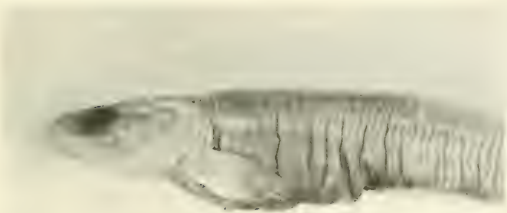


FIGURE 4. *Pachycara suspectum* (Garman), SIO 68-106, 218 mm SL, from the Gulf of California.

PARATYPES.—British Columbia: BCPM 980-121 (1); same as holotype. BCPM 979-11365 (2); W of Tasu Sound; trap, 2,744 m; EASTWARD HO set 5; 16 Aug. 1979. BCPM 979-11369 (6); W of Tasu Sound; trap, 2,889 m; EASTWARD HO set 12; 22 Aug. 1979. BCPM 980-100 (1); W of Tasu Sound; trap, 2,926 m; EASTWARD HO set 18; Aug. 1979. USNM 221113 (1); recat. from BCPM 979-11369. NMC 86-0444 (1); W of Tasu Sound; trap, 2,743–2,926 m; EASTWARD HO set 11; 21 Aug. 1979. Cascadia Abyssal Plain: CAS 60524 (1); 45°18.7'–18.5'N, 126°34.4'–28.6'W; trawl, 2,750 m; YA-QUINA sta. CP-2C, BMT 265; 18 Feb. 1971. CAS 60525 (1); 45°21.5'–21.7'N, 127°33.0'–38.5'W; trawl, 2,800 m; YA-QUINA sta. CP-3C, BMT 280; 18 May 1971. California: OSUO 2558 (1); Mendocino Ridge; 40°45.8'N, 127°31.6'W; trap, 3,225 m; USGS S. P. LEE sta. L2-86-5T; 20–21 July 1986. SIO 67-121 (36); SW of Cordell Bank; 37°57.4'N, 123°40.5'W; trap, 2,707–3,219 m; THOMAS WASHINGTON; 16–17 June 1967. Mexico: SIO 65-69 (3); off Guadalupe Isl., 4 mi E of southern tip; trap, 1,829 m; 4–5 Mar. 1965. SIO 68-120 (6); Gulf of California; 25°35.4'N, 109°46.0'W; trap, over 1,728 m; THOMAS WASHINGTON; 24–25 Jan. 1968. SIO 70-12 (3); off Baja California Norte; 31°10.0'–06.9'N, 118°52.6'–53.4'W; trap, 2,524 m; MELVILLE; 16–17 Dec. 1969.

ADDITIONAL MATERIAL.—SIO 66-19 (2); off Guadalupe Isl., Mexico; 29°07.8'N, 118°12.5'W; trap, 2,378 m; ALEXANDER AGASSIZ; 1–2 Apr. 1966.

DIAGNOSIS.—A species of *Pachycara* as defined by Anderson (1984) distinguished by the following combination of characters: pelvic fins present, their lengths 4.8–11.3% HL; mediolateral branch of lateral line originating in pectoral axil just posterior to vertical through pectoral

base; scales absent on nape, or, if present, not extending anterior to line connecting anterodorsal edges of gill slits; pectoral fin length 63.0–70.8% HL; vertebrae 28–31 + 73–80 = 102–109; head length 12.0–15.6% SL; anal fin origin associated with vertebrae 27–31.

DESCRIPTION.—Counts and measurements presented in Table 1 were compiled from all known specimens, 76–422 mm SL (including one gravid female). The following description is based on 10 adult males, nine adult females, 42 juveniles of both sexes, and two eviscerated adults. Head large, ovoid, wider in adults than juveniles. Body short, deep, broader in cross section in adults than juveniles. Tail laterally compressed, more so posteriorly, tapering gradually to tip. Skin firm, not gelatinous, but pliable around head, especially near mouth, cheeks and nape, owing to subdermal lipid layer. Scales minute, cycloid, imbedded, covering body, tail and vertical fins to about half their height; usually no scales on nape, but when present, restricted to small patches immediately anterior to dorsal fin origin, or, rarely, extending anteriorly to line connecting anterodorsal edges of gill slits. Scales usually absent on pectoral base, when present, usually in irregular, ovoid patch not extending from dorsal to ventral margin of fin and not extending onto fin more than 15% of its length. Scales on right cheek in small patch between preoperculum and mandibular pores seven and eight in one specimen (SIO 67-121, 235 mm SL female), scales otherwise absent on head. No scales developed in smallest specimen, 76 mm SL. Eye circular, larger in proportion to head in small specimens than largest adults. Gill slit somewhat shortened, usually extending ventrally to just above ventral margin of pectoral base, but restricted to mid-height of pectoral base in a few specimens, and extending to below ventral margin of pectoral base in a few others. Slight, rounded or squared-



PDB

FIGURE 5. *Pachycara gymminium* n. sp., USNM 280121 (holotype, 422 mm SL), off the Queen Charlotte Islands, British Columbia.

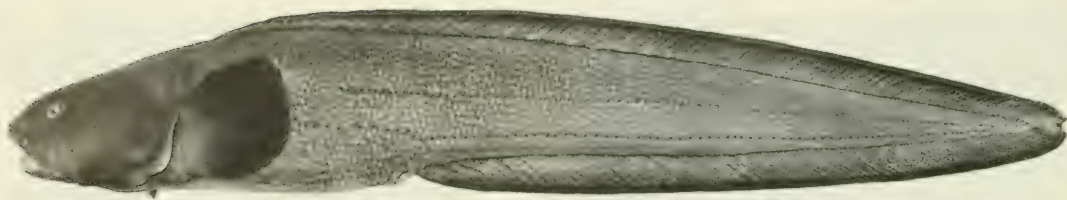


FIGURE 6. *Pachycara lepinium* n. sp., USNM 280120 (holotype, 465 mm SL), off the Queen Charlotte Islands, British Columbia.

off, posteriorly-directed lobe formed at dorsal margin of operculum, its dorsalmost margin usually straight, but deeply concave in one specimen. Single pair of nostrils at snout tip, nasal tube very short, usually not reaching upper lip (reaching upper lip only in few juveniles less than 220 mm SL). Pectoral fin large, its origin just below body midline; posterior margin nearly evenly rounded (except in few injured specimens); ventralmost 3–5 rays shorter and thicker than others, their tips not at all, or just slightly exerted; pectoral rays usually 15–16 (Table 2).

Mouth terminal, upper jaw slightly longer in relation to head in adult males than comparably sized adult females; upper jaw 40.5–52.8% HL ($\bar{x}$ = 43.9%, n = 12) in males over 280 mm SL, 37.7–41.8% HL ($\bar{x}$ = 39.5%, n = 11) in females over 295 mm SL. Minute, epidermal prickles on anterior portions of lips and chin, these often nearly rubbed off in large specimens. Palatine membrane (oral valve) moderately developed, almost reaching anterior margin of vomer in most specimens. Teeth in jaws and palate small, conical, dentition not sexually dimorphic. Jaw teeth in single row anteriorly in smallest specimens, in 4–5 anterior rows in adults, blending into single posterior row in all. Vomerine teeth in irregular patch or arched row; palatine teeth in single row.

Cephalic lateralis pore system reduced, numerical variation in pores of postorbital and suborbital canals only. Postorbital pores one, three, and four present on both sides in one specimen; pores one and four only present in 18; pores one and four on one side, pores one, three, and four on the other in nine specimens. Two pairs of nasal pores, one set mesial to nasal tube, the other posteromesially. Usually six suborbital pores, all emanating from ventral ramus of suborbital bone chain, but a seventh pore emanating from ascending ramus behind eye just below first postorbital pore in seven specimens, and, in one,

from just above sixth pore on cheek. Eight preoperculo-mandibular pores, four emanating from dentary, one from angulo-articular, and three from preopercle. Interorbital and occipital (supratemporal) pores absent. Body lateral line of two branches: mediolateral, originating in pectoral axil on vertical through pectoral base, complete to tail tip, and ventral, originating just posterior to fourth postorbital pore, coursing gradually across body to just above anus, then running to tail tip above anal fin base.

Vertebrae symmetrical, no geographical variation exhibited numerically. Caudal fin rays variable, with one or two epural, 4–6 upper hypural, and 4–5 lower hypural rays. Last anal ray associated with second preural vertebra, last dorsal ray associated with fourth preural vertebra. Dorsal fin origin associated with vertebrae 3–5, with no free pterygiophores. All dorsal elements soft rays, first one not segmented, but bilaterally divided at least near base. Anal fin origin associated with antepenultimate to ultimate precaudal vertebrae, with 3–5 pterygiophores inserted anterior to haemal spine of first caudal vertebra.

Gill rakers short, roughly triangular in adults, more slender, but not pointed, in smallest specimens; adults with 3–5 epibranchial rakers and usually 11–13 on ceratobranchial; raker denticles absent. Branchiostegal rays six: four articulating with ceratohyal and two with epihyal. Two nub-like pyloric caeca, not appreciably longer in smallest specimens than largest. Pseudobranch filaments relatively long, about one eye diameter in length (or more in smallest specimens), numbering 3–5.

Fresh specimens uniformly dark brown, head and pectoral fin darker, almost black. Lining of orobranchial chamber dark brown or black. Margins of vertical fins and peritoneum black.

One gravid female known (CAS 60524, 350 mm SL), with 80 ova 5.2–7.2 mm in diameter ($\bar{x}$ = 5.8 mm). Stomach contents of several spec-

imens consisted of amphipods, isopods, polychaetes, and trap bait.

DISTRIBUTION.—Off the Queen Charlotte Islands, British Columbia, south to off Guadalupe Island, Mexico, and in the Gulf of California in 1,829–3,219 m over brown and green mud bottoms.

ETYMOLOGY.—From the Greek *γυμνός* (naked) and *λίον* (nape) in reference to the species' scaleless head.

Pachycara lepinium n. sp.

(Figure 6)

Lycodes sp. Hubbs et al., 1979:14.

Lycenchelys "D." Percy et al., 1982:387.

HOLOTYPE.—USNM 280120 (male, 465 mm SL); British Columbia, W of Tasu Sound, Queen Charlotte Islands; 52°38.0'N, 132°05.8'W; trap, 2,744 m; TALAPUS set 8; 4 Feb. 1980.

PARATYPES.—British Columbia: BCPM 980-121 (1); same as holotype. BCPM 980-98 (1); W of Tasu Sound; trap, 2,889 m; EASTWARD HO set 6; Aug. 1979. NMC 86-0445 (1); W of Tasu Sound; trap, 2,744 m; EASTWARD HO set 5; 16 Aug. 1979. USNM 221114 (1); W of Tasu Sound; trap, 2,889 m; EASTWARD HO set 12; 22 Aug. 1979. Cascadia Abyssal Plain: CAS 60526 (1); 44°23.0–25.4'N, 125°34.0–35.0'W; trawl, 2,878 m; YAQUINA sta. CP-1F, BMT 410; 4 Aug. 1974. CAS 60527 (1); 45°46.9–45.7'N, 126°35.5'W; trawl, 2,665 m; YAQUINA sta. CP-2A, BMT 259; 15 Feb. 1971. CAS 60528 (1); 44°41.7–43.6'N, 125°33.5–32.5'W; trawl, 2,825 m; YAQUINA sta. CP-1E, BMT 120; 6 Oct. 1969. CAS 60529 (1); 45°53.1–51.8'N, 126°39.0–42.5'W; trawl, 2,713 m; YAQUINA sta. CP-2A, BMT 154; 16 Jan. 1970. CAS 60530 (1); 44°29.6–45.2'N, 126°29.0–35.9'W; trawl, 2,818 m; YAQUINA sta. CP-2D, OTB 90; 23 Oct. 1965. OSUO 2563 (1); 45°09.3–10.5'N, 125°38.3–38.0'W; trawl, 2,669 m; YAQUINA sta. CP-1C, BMT 93; 15–16 July 1969. LACM 44315-1 (1); 44°39.7–39.0'N, 126°39.6–44.8'W; trawl, 2,816 m; CA-YUSE sta. CP-2E, BMT 253; 30 Sept. 1970. California: SIO 66-50 (1); off Cape Mendocino; 40°34.6–34.7'N, 125°51.4–51.5'W; trap, 2,970 m; ALEXANDER AGASSIZ; 21–22 May 1966. SIO 60-475 (1); off Farallon Isl.; trawl, ca. 1,800 m; 10 Nov. 1960. SIO 59-288 (1); San Clemente Basin; 32°39.0'N, 118°09.3'W; trap, 2,027 m; 23–24 July 1959. SIO 59-289 (3); San Clemente Basin; 32°39.0'N, 118°09.3'W; trap, 2,023 m; 23–24 July 1959. SIO 65-452 (4); San Clemente Basin; 32°38.7'N, 118°08.4'W; trap, 2,008 m; ALEXANDER AGASSIZ; 25 Sept. 1965. LACM 32114-2 (1); San Clemente Basin; 32°38.0–37.5'N, 118°09.0–06.4'W; trap, 1,829–1,939 m; VELLERO IV sta. 12521; 10 Dec. 1968. Mexico: SIO 59-365 (5); off Cabo Colnet; 31°02.7'N, 116°59.0'W; trap, 2,140 m; 27–28 Oct. 1959.

ADDITIONAL MATERIAL.—SIO 59-364 (1); off Cabo Colnet, Mexico; 31°00.5'N, 118°06.0'W; trap, 1,728 m; 27 Oct. 1959. SIO 59-366 (1); off Cabo Colnet, Mexico; 31°02.7'N, 116°59.3'W; trap, 2,140 m; 27–28 Oct. 1959.

DIAGNOSIS.—A species of *Pachycara* as defined by Anderson (1984) distinguished by the following combination of characters: pelvic fins

present, their length 11.5–17.3% HL; mediolateral branch of lateral line originating posterior to pectoral fin margin; scales present on nape, extending to interorbital region; pectoral fin length 72.5–89.9% HL; vertebrae 23–26 + 80–94 = 105–120; head length 13.8–15.9% SL; anal fin origin associated with vertebrae 23–26.

DESCRIPTION.—Counts and measurements presented in Table 1 were compiled from all known specimens, 221–597 mm SL (including one gravid female). The following description is based on six adult males, eight adult females, and 16 juveniles of both sexes. Head large, ovoid, wider in adults than juveniles. Body relatively short, deep, broader in cross section in adults than juveniles. Tail laterally compressed, more so posteriorly, tapering gradually to tip. Skin firm, not gelatinous, but somewhat pliable around head, especially near mouth and cheeks, due to subdermal lipid layer. Scales minute, cycloid, imbedded, covering body, tail, and vertical fins almost to their margins; scales on nape extend anteriorly to vertical one eye diameter anterior to dorsalmost edge of gill opening in smallest specimen, to interorbital region in adults. Scales present in pectoral axil and on base, extending on outer surface of fin to half or more its length; scales present on cheeks. Eye circular, relatively larger in proportion to head in smallest specimens than largest. Gill slit long, extending ventrally almost to pelvic fin origin; slight, rounded, posteriorly-directed lobe formed at dorsal margin of operculum. Single pair of nostrils at snout tip, nasal tube very short, not reaching upper lip. Pectoral fin large, its origin just below body midline; posterior margin almost evenly rounded; lowermost 5–6 rays shorter and thicker than others, their tips somewhat excised; pectoral rays usually 17–18 (Table 2).

Mouth subterminal in largest adults, terminal in young; upper jaw longer in relation to head in adult males than comparably sized adult females; upper jaw 48.8–52.0% HL ($\bar{x}$ = 50.3, n = 5) in males over 380 mm SL, 41.7–46.4% HL ($\bar{x}$ = 44.8%, n = 7) in females over 380 mm SL. Minute, epidermal prickles on anterior portions of lips and chin. Palatine membrane (oral valve) well developed, reaching anterior edge of vomer. Teeth in jaws and palate small, conical; dentition not sexually dimorphic. Jaw teeth in two irregular rows anteriorly in smallest specimens, in 4–5 anterior rows in adults, blending into single posterior row in all. Vomerine teeth in irregular

patch; palatine teeth in one or two (largest specimens) irregular rows.

Cephalic lateralis pore system reduced, numerical variation present only in pores of post-orbital canal. Postorbital pores one, three, and four present, emanating from frontal, pterotic and lateral extrascapular, respectively; pores one and four only in two specimens; pores one and four on one side, one, three, and four on the other in two other specimens. Two pairs of nasal pores, one set mesial to nasal tube, the other set posteromesially. Six suborbital pores, all emanating from ventral ramus of suborbital bone chain. Eight preoperculomandibular pores, four emanating from dentary, one from anguloarticular, and three from preopercle. Interorbital and occipital (supratemporal) pores absent. Body lateral line of two branches: mediolateral, originating at or just posterior to pectoral fin margin, complete to tail tip, and ventral, originating just posterior to fourth postorbital pore, coursing gradually across body to just above anus, then running just above anal fin to tail tip.

Vertebrae symmetrical. Individuals from basins of southern California and northern Baja California with significantly more vertebrae than those from the north (specimens from British Columbia to Cape Mendocino with 105–110 vertebrae [$n = 13$, $\bar{x} = 107.2$, $SD = 1.58$], specimens from the Farallon Islands to Baja California with 116–120 vertebrae [$n = 16$, $\bar{x} = 117.2$, $SD = 0.49$]). Caudal fin rays variable, with two epural, 3–5 upper hypural and 3–5 lower hypural rays. Last anal ray associated with second preural vertebra, last dorsal ray associated with third or fourth preural vertebrae. Dorsal fin origin associated with vertebrae 4–5, with no free pterygiophores. All dorsal fin elements soft rays, first 1–2 not segmented, but bilaterally divided at least near base. Anal fin origin associated with antepenultimate to ultimate precaudal vertebra, with 2–5 pterygiophores inserted anterior to haemal spine of first caudal vertebra.

Gill rakers short, roughly triangular, relatively longer on dorsal portion of ceratobranchial; largest adults with four epibranchial rakers and 13–15 on ceratobranchial; raker denticles absent. Branchiostegal rays six: four articulating with ceratohyal and two with epihyal. Two nubile pyloric caeca, not appreciably longer in smallest specimens. Pseudobranch filaments relatively long, about one eye diameter in length in both adults and juveniles, numbering 2–5.

Fresh specimens uniformly dark brown, head and pectoral fin darker, almost black. Lining of orobranchial chamber dark brown or black. Margins of vertical fins and peritoneum black.

One gravid female, 412 mm SL (SIO 59-364, ovary somewhat damaged), had ova averaging 4.3 mm in diameter. Stomach contents of several specimens included polychaetes, bivalves, and amphipods.

DISTRIBUTION.—Off the Queen Charlotte Islands, British Columbia, south to off Guadalupe Island, Mexico, at depths of 1,728–2,970 m over brown and green mud bottoms. Often taken in traps and trawls with *P. gymninium*, but this species not yet known from the Gulf of California.

ETYMOLOGY.—From the Greek *λεπίς* (scale) and *ινίον* (nape) in reference to the species' scaly head.

DISCUSSION

The distribution of *P. bulbiceps* may at first glance appear anomalous, in that the species is widely distributed in the North Atlantic, but otherwise restricted to the northeastern Pacific continental rise and adjacent abyss. Anderson (1988) provided evidence that the pan-American, tropical, abyssal fish fauna was sundered by tectonic uplifting in the region of the Panamanian isthmus at least by the mid-Miocene. The present Caribbean deep-water ichthyofauna is very different from that of the eastern tropical Pacific (Garman 1899; Anderson et al. 1986). Thus, the Pacific and Atlantic stocks of *P. bulbiceps* would have had ample time to speciate if there were no South Atlantic–South Pacific populations linking the northern groups. Because abyssal trawl samples from the southwestern Atlantic and southeastern Pacific are generally lacking for most regions, isolation of the northern populations cannot be evaluated. Based on the paleogeography of the American tropics cited by Anderson (1988), the Atlantic and Pacific populations probably are not isolated from each other, and future abyssal collections off Chile, Argentina, Brazil, and probably southern Africa should produce specimens of *P. bulbiceps*. Among the characters presented in Table 1, as well as traditional data analysis used by us before (Peden and Anderson 1978; Peden 1981; Anderson 1982), including features of the axial skeleton, gill arches, dentition, squamation, and lateral lines, no numerical or morphological differences were de-

tected between the Atlantic and Pacific populations, thus isolation seems improbable. This is in contrast to North Atlantic and North Pacific populations of the grenadier *Coryphaenoides armatus*, which exhibited minor electrophoretic but significant biometric differences, resulting in Wilson and Waples' (1984) placement of these forms as separate subspecies. Similarly, Small (1981) found specific differences in the cosmopolitan bathyal genus *Antimora* and recognized an endemic North Pacific species (*A. microlepis*), while a second species (*A. rostrata*) was shown to be circumglobal but excluded from the North Pacific.

The geographic variation noted for *P. lepinium*, but not found in *P. gymninium*, is difficult to explain, but may relate to differing environmental conditions that affect vertebral number in the basins of the Southern California Bight. Still, no variation was noted in the eight individuals of *P. gymninium* from this area, or in *P. bulbiceps* along its entire range. If the distributions of these species are broader than present samples reflect (and they probably are), significant geographic variation may be found when adequate material is analyzed along the ranges of all species, as was found for the eelpouts *Lycodapus mandibularis* (Peden 1979) and *Lycodes diapterus* (Peden 1981). The lack of variation noted for *P. gymninium* may be due to either the present poor sample size or is a valid specific character, as found in another eelpout genus, *Gymnelus* (Anderson 1982).

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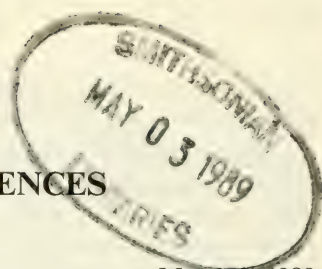
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March 9, 1989

THE HARVESTMEN FAMILY PHALANGODIDAE.
1. THE NEW GENUS *CALICINA*, WITH NOTES ON *SITALCINA*
(OPILIONES: LANIATORES)

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ABSTRACT: The Californian phalangodid genus *Sitalcina* Banks is shown to be polyphyletic, and is restricted to include only those species closely related to the type species *Sitalces californica* Banks. A new genus, *Calicina*, described to accommodate most of the remaining species, is defined by the presence of a tarsal spur on the male palpus, penis glans with apically directed stylus, ovipositor with double row of apical setae, and ovipositor cuticle with microspines. At least the first of these characters is a synapomorphy.

Of the 25 species of *Calicina* recognized, 18 are transferred from *Sitalcina*: *breva* Briggs (elevated from subspecies), *cloughensis* Briggs and Hom, *digita* Briggs and Hom, *ensata* Briggs, *kaweahensis* Briggs and Hom, *keenea* Briggs, *macula* Briggs, *mariposa* Briggs, *minor* Briggs and Hom, *morroensis* Briggs, *palapraeputia* Briggs, *piedra* Briggs, *polina* Briggs, *sequoia* Briggs and Hom, *serpentinea* Briggs and Hom, *sierra* Briggs and Hom, *topanga* Briggs, and *yosemitensis* Briggs. The remaining species are new: *arida*, *basalta*, *conifera*, *diminua*, *dimorphica*, *galena*, and *mesaensis*.

Based on genitalic characters, primarily glans structure, four species groups and nine subgroups are recognized. Their relationships are hypothesized using cladistic analysis and vicariance biogeography. The distribution of *Calicina* is strongly concordant with that of the slender salamander, *Batrachoseps*, and with the presumed distributions of exotic terranes.

Interspecific variation in the somatic morphology of *Calicina* appears to be the result of paedomorphosis and troglobism. These modifications, present in most species, are probably adaptations to xeric environments and, possibly, competition with other phalangodids.

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INTRODUCTION

A major problem in the systematics of harvestmen is the apparent scarcity of reliable generic characters. This stems largely from the classic studies of Roewer (e.g., 1923) which over-emphasized the importance of easily visible somatic characters, such as variation in the tarsal count, in defining genera. This practice has resulted in a confusing proliferation of small and monotypic genera. For example, the 17 known species of the eastern Nearctic Phalangodidae are currently assigned to eight genera (Goodnight and Goodnight 1942, 1967).

In sharp contrast to this general trend is the treatment of the phalangodids of California: only two genera are recognized for an unusually rich fauna of 39 described species. One of these, *Banksula* Roewer, includes strictly cavernicolous species having uniformly high tarsal counts (4-6-5-6) and the other, *Sitalcina* Banks, contains epigean species with lower counts (3-5-5-5 or less). Recent studies (Briggs 1974; Briggs and Ubick 1981) have demonstrated that *Banksula* is well defined by both somatic and genitalic characters: the palpal femur is armed with dorsal spines and the penis has a bifurcate ventral plate. On the other hand, Briggs (1968) found no derived character uniting the 29 species of *Sitalcina*. He even commented on the heterogeneity of the genus, listing interspecific differences in size, tarsal count, presence or absence of eyes, and type of sexually dimorphic structures. He tentatively arranged the species into three groups: (1) those with sexually dimorphic trochanters, (2) those with sexually dimorphic palps, and (3) those lacking sexual dimorphisms. However, in the absence of additional characters and because of the overall somatic similarity of the species, he did not question the validity of the genus.

Our present investigations of the genitalic morphology of *Sitalcina* indicate that the genus is indeed polyphyletic. The strongest evidence comes from the morphology of the penis where, on the basis of the glans structure, two groups of species are evident. The first is characterized by a folded, caudally directed glans that swings open 180° along a dorsoapical arc during expansion (Fig. 1b). The second is characterized by an apically directed glans that expands by a rectilinear, telescoping movement out of the shaft (Fig. 6f, g). Such striking genitalic differences are com-

parable to those used to distinguish families (Martens 1986).

It is now evident that *Sitalcina* must be restricted to include only those species closely related to the type species, *Sitalces californica* Banks. This monophyletic group, corresponding to group "1" of Briggs (1968), is defined by the characters listed in Table 1. In addition to the folding glans, all *Sitalcina* males have trochanteral spurs on leg IV (Fig. 1a). The ovipositor of *Sitalcina* is distinctive in various features, of which the imbricate cuticle sculpturing is possibly synapomorphic.

The nine species that now comprise *Sitalcina* (along with three others still unplaced that apparently belong to other genera) will be treated in a future paper. The purpose of this study is to describe the new genus represented by the remaining species, for which we propose the name *Calicina*. The species of *Calicina* are revised and their morphological and spatial relationships hypothesized using cladistics and vicariance biogeography. Analyses of natural history and ecology are provided.

MATERIALS AND METHODS

The 800 specimens examined during the course of this study were collected almost exclusively by Briggs and associates over the past two decades. Specimens from early collections were originally stored in Oudemans' Fluid, which gave excellent initial preservation (Briggs 1968:3). However, it is now evident that prolonged storage in this solution (about 10 years or more) discolors the specimens, results in deterioration of the internal tissues, and makes genitalic extraction difficult. By comparison, specimens preserved in 75% to 85% ethanol for much longer periods do not show signs of such damage.

The genitalia can usually be extracted by simply opening the operculum and squeezing the abdomen with forceps. When this fails it is necessary to push out the genitalia carefully with a probe inserted into the anal region or, as a last resort, to dissect it out of the body cavity. Males often require additional treatment with KOH in order to fully expand the glans, which normally lies retracted within the shaft. For this, entire specimens are soaked in cold 10% KOH solution for about two minutes and then transferred to a water bath where, aided by gentle squeezing of the abdomen, maximum expansion can occur.

TABLE 1. COMPARATIVE MORPHOLOGY OF *SITALCINA* AND *CALICINA*.

	<i>Sitalcina</i>	<i>Calicina</i>
Total length	1.50–2.40 mm	0.77–1.67 mm
Eyes	present	present or absent
Tarsal count	3-5-5-5	3-5-5-5 to 3-3-4-4
Palp		
Patella	3 spine-bearing tubercles	2 spine-bearing tubercles
Tarsus (♂)	unmodified	with spur (usually)
Leg IV		
Trochanter (♂)	with spur	unmodified
Penis		
Glans	folding	telescoping
Ovipositor ¹		
Shape	bent	straight
Cuticle	imbricate ²	with microspines
Apical setae		
Shape	apically hooked ³	evenly bent
Length	long—cross at center	shorter
Number	12–20	12, rarely 14 or 16
Arrangement	not grouped ⁴	in triads
Subapical setae		
Number	none	1–3 pairs, rarely none

¹ Species of *Sitalcina* examined: *californica*, *borregoensis*, *madera*, *scopula*, and *sura*.

² In *S. californica*.

³ Except *S. scopula*.

⁴ Except *S. sura*.

Unless otherwise indicated, the specimens examined during this study, including all primary types, are deposited at the California Academy of Sciences. Additional specimens are from the collections of the American Museum of Natural History (AMNH) and the University of California at Berkeley (UCB).

Complete species descriptions are given for new species; additional descriptions for those treated by Briggs (1968). All specimen measurements are in millimeters.

ABBREVIATIONS FOR COLLECTORS

- AGG—Andy G. Grubbs
- AK—Albert Kurz
- AKSJ—Albert K. S. Jung
- AL—Albert Lee
- BL—Benton Leong
- BM—Barbara Martin
- CF—C. Fox
- DB—D. Broussard
- DCR—D. Craig Rudolph
- DR—David Rentz
- DU—Darrell Ubick

- EVI—E. VanIngen
- GAM—G. A. Marsh
- GL—Galen Leung
- GT—Gordon Tang
- JG—Joseph Gee
- JRH—J. R. Helfer
- JSB—J. S. Buckett
- KH—Kevin Hom
- KK—K. Kay
- LMS—L. M. Smith
- MG—Michael Gardner
- MM—M. McEachern
- MW—Michael Wong
- NB—N. Boice
- RL—Robert Lem
- ROS—Robert O. Schuster
- SK—S. Kubota
- SO—Stefan Ong
- SW—Steve Winterath
- TO—Toshiro Ohsumi
- TSB—Thomas S. Briggs
- VFL—Vincent F. Lee
- WCR—Warren C. Rauscher
- WES—Warren E. Savary
- WI—Wilton Ivie

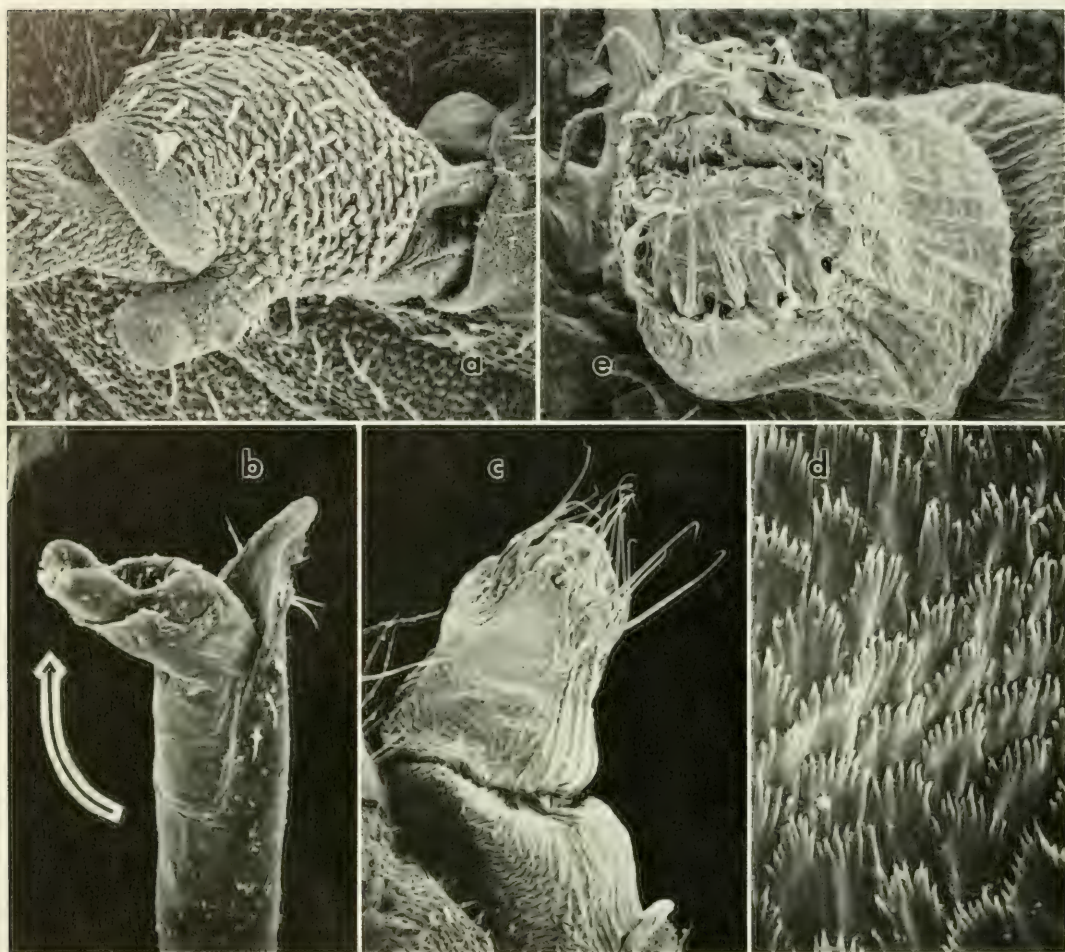


FIGURE 1. *Sitalcina californica*. (a) Trochanter IV of male, lateral view (180 $\times$). (b) Expanded glans penis, sublateral view (240 $\times$). Arrow indicates movement of glans during expansion. (c) Ovipositor, lateral view (180 $\times$). (d) Ovipositor, close-up of lateral surface showing imbricate cuticle (1,800 $\times$). (e) Ovipositor, apical view (300 $\times$).

TAXONOMY

Family PHALANGODIDAE Simon
Subfamily PHALANGODINAE Simon

Calicina Ubick and Briggs, new genus

DIAGNOSIS.—Males of *Calicina* are unique among the Nearctic phalangodid genera in having a telescoping penis glans (as opposed to a folding one). Additionally, most males of *Calicina* have a dorsal spur on the palpal tarsus, which is not known in other phalangodids. Females are distinct from those of *Sitalcina*, and possibly other genera, in having ovipositors with a double setal fringe and a cuticle with microspines. Most species of *Calicina* may be distinguished from

other phalangodid genera by their reduced tarsal counts of less than 3-5-5-5.

TYPE SPECIES.—*Sitalcina mariposa* Briggs, 1968.

ETYMOLOGY.—The generic name is a contraction of California *Sitalcina* and is feminine in gender.

DESCRIPTION.—Body length 0.77–1.67. Color ranges from pale yellow to orange to reddish-brown. Body cuticle minutely and densely tuberculate, with scales, setae, and nipplelike tubercles. Scute with prominent ocular tubercle at anterior margin; varying in size, shape, and degree of rugosity (see Briggs 1968, fig. 45–57, 59, 62, 63, 65, 66). Eyes well developed (Fig. 3a) or reduced, lacking retina and occasionally cornea

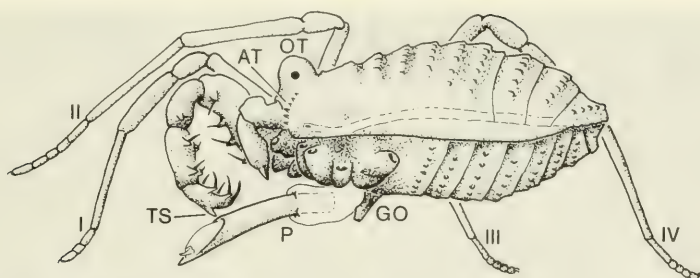


FIGURE 2. *Calicina mariposa*, lateral view of male (left appendages omitted). AT = anterior tubercles, OT = ocular tubercle, TS = tarsal spur of palpus, GO = genital operculum, P = penis, legs numbered.

(=lens) (Fig. 3b). Carapace with two rows of anterior tubercles numbering from 0 to 4 or rarely to 8 pairs (Fig. 2, 3a, b). Ozopore well developed, on anteriolateral margin, with distinct posterior channel. Tergites I–V fused, VI–VIII free, with median, transverse row of tubercles interspersed with short setae. Venter textured similarly as scute but more densely setose; seven free sternites with median, transverse rows of tubercles. Genital operculum between coxae IV, apically truncate in males, rounded in females. Coxae I and II with endites.

Leg sculpturing consisting of minutely tuberculate scales; calcani and tarsi smooth. Leg II longest, leg length formula (longest to shortest) II, IV, I, III. Tarsal counts 3-5-5-5, 3-4-4-5, or 3-4-4-4; rarely 3-5-4-5 or 3-3-4-4. Tarsal claws single on legs I and II; paired on legs III and IV. Juveniles with hind claws on onychium, arolium between paired claws. Palpi and chelicerae distally setose, with smooth cuticle of appressed scales. Palpi robust, ventrally armed with spine-bearing tubercles (femur with three ectobasally and one mesodistally; patella with 1 pair; tibia and tarsus with 2 pairs each) (Fig. 3c). Male palpal tarsus with a well developed dorsal spur (Fig. 4a), with vestigial spur (Fig. 4b), or without spur; occasionally with enlarged mesal spine-bearing tubercle (Fig. 4c, d).

Penis without muscles, composed of basal sac, shaft, and apical glans. Basal sac inflatable. Shaft (=truncus) cylindrical, sclerotized; length 3.5–7 × width; apicoventral part (=ventral plate) rounded or attenuated, set with setae. Glans telescoping, with basal segment and stylus, rarely with additional (middle) segment (*palapraeputia*). Collar lobes (= ?*Titillator* of Martens 1986) on basal segment (*mariposa* and *digita* groups), on middle segment (*palapraeputia*), or apparently absent (*serpentinea* group). Stylus apical

and variable in shape. Accessory structures either thin, scalelike parastyli (= ?*Konduktor* of Martens 1986) (*digita* group) or robust, lobed dorsal process (*serpentinea* group).

Ovipositor short, straight, and cylindrical when expanded; length 1.5–2.0 × width; divided into basal and distal segments. Lateral and/or apical surface covered with minute, pointed tubercles (microspines). Apex with 2 or 4 lobes, occasionally with dorsal folds; with setal fringe of 12 apical setae (10 in *diminua*) grouped in triads and 1–4 pairs of subapical setae (most species) or with 14 apical setae only (*palapraeputia* and *serpentinea* subgroup); occasionally with a pair of apical teeth (Fig. 5).

DISTRIBUTION AND SPECIES.—The genus *Calicina* is found only in the central Sierra Nevada and the Coast Ranges of California. The 25 known species represent four species groups and nine subgroups.

Key to the *Calicina* Species Groups and Subgroups

Based on Characters of the Male Genitalia

1. Basal glans segment with a pair of collar lobes (Fig. 16a–d) 2
 - Basal glans segment without collar lobes (Fig. 16e–h) 7
2. Parastyli absent (Fig. 6, 10a–d) 3
 - Parastyli present (Fig. 7–9, 10e–h) (*digita* group) 4
3. Collar lobes simple (Fig. 6)
 - *mariposa* group and subgroup
 - Collar lobes bilobed (Fig. 10a–d)
 - *arida* subgroup, in part (*cloughensis*)
4. Parastyli ventral (Fig. 7) *digita* subgroup
 - Parastyli lateral or dorsal 5
5. Parastyli lateral, broad and ornate (Fig. 8)
 - *kaweahensis* subgroup

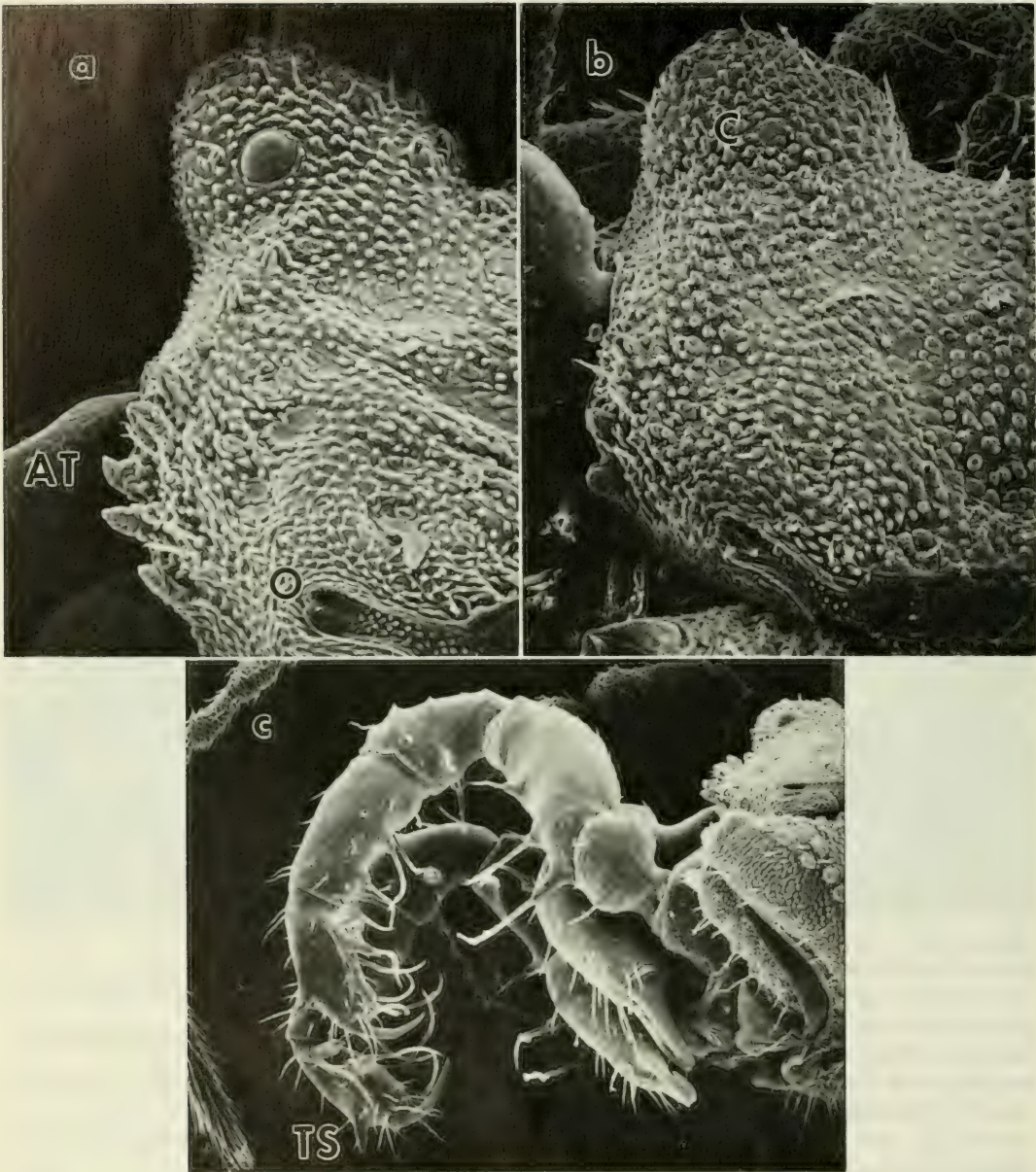


FIGURE 3. *Calicina*, morphology. (a) *C. mariposa*, male paratopotype, anterior part of scute showing ocular tubercle with large cornea, a row of paracuticular anterior tubercles (AT), and the ozopore (O) (230×). (b) *C. serpentinea*, female, same view showing reduced number of anterior tubercles and degenerate cornea (C) (230×). (c) *C. mariposa*, male paratopotype, chelicerae and palpi showing tarsal spurs (TS) (80×).

- Parastyli dorsal, narrow 6
- 6. Parastyli separate; stylus straight; ventral plate acuminate (Fig. 9) *topanga* subgroup
- Parastyli fused; stylus sinuous; ventral plate unmodified (Fig. 10e-h)
- *arida* subgroup, in part (*arida*)
- 7. Middle segment of glans completely surrounding stylus; collar lobes hornlike (Fig. 11) *palapraeputia* group and subgroup
- Middle segment of glans forming the dorsal process that is distinct from stylus; lobes variable (Fig. 16g, h) ... (*serpentinea* group) 8



FIGURE 4. *Calicina*, male palpal tarsi. (a) *C. mariposa*, showing large tarsal spur (310 $\times$). (b) *C. mesaensis*, showing reduced tarsal spur (310 $\times$). (c) *C. minor*, showing enlarged mesobasal spine-bearing tubercle (X) (470 $\times$). (d) *C. ensata*, showing enlarged mesoapical spine-bearing tubercle (X) (310 $\times$).

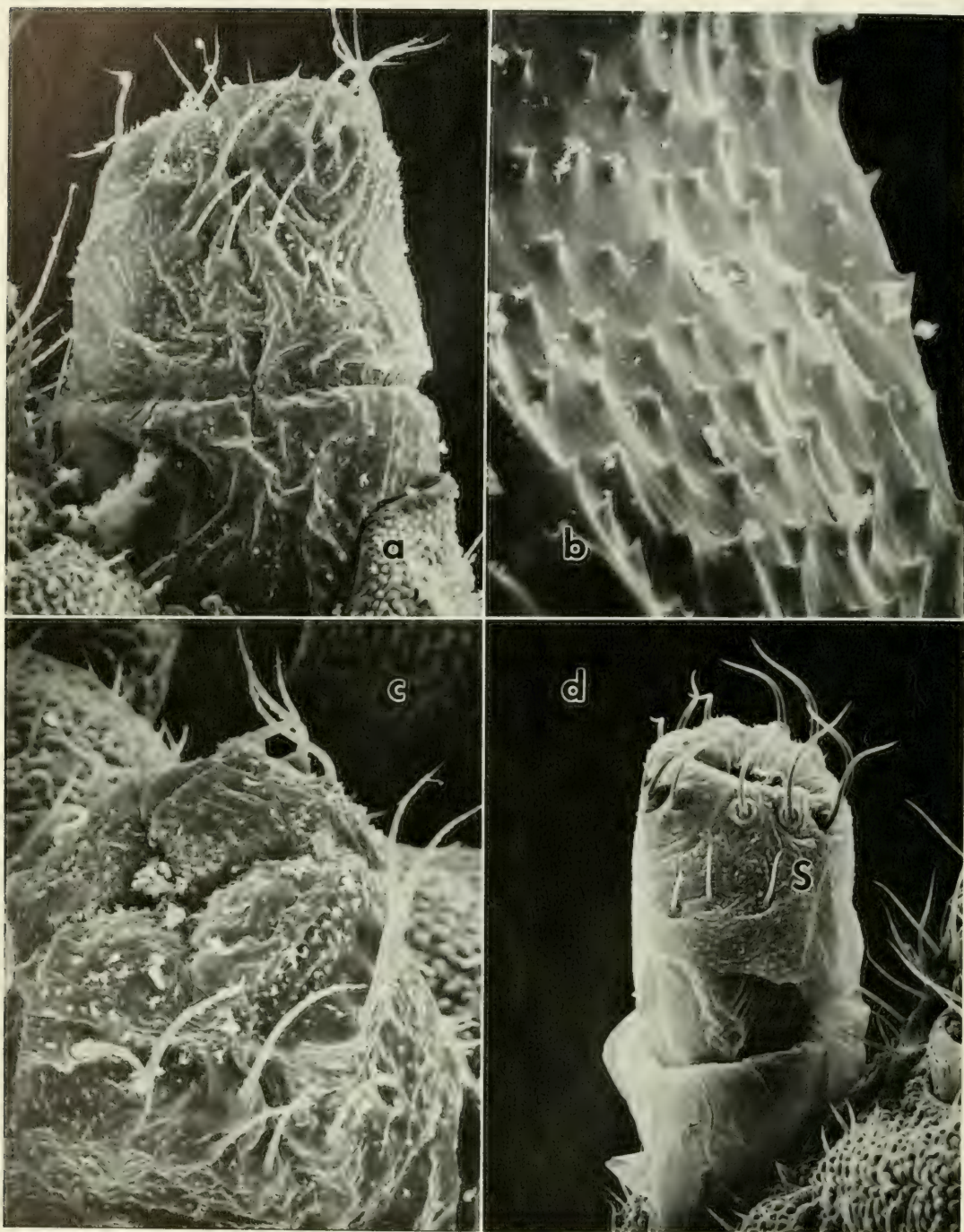
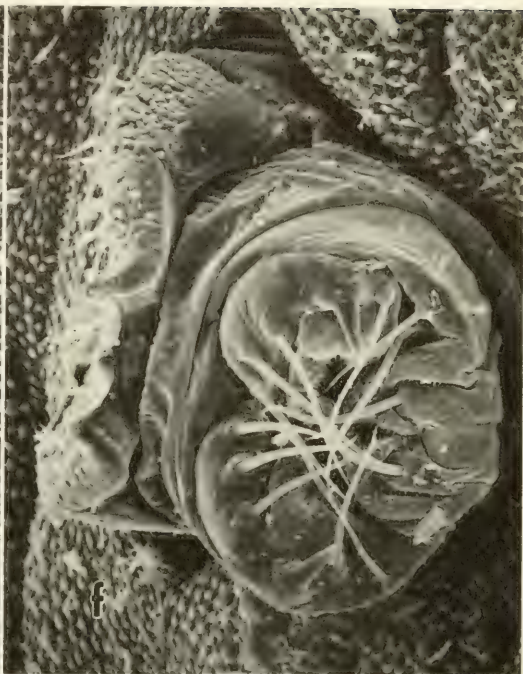
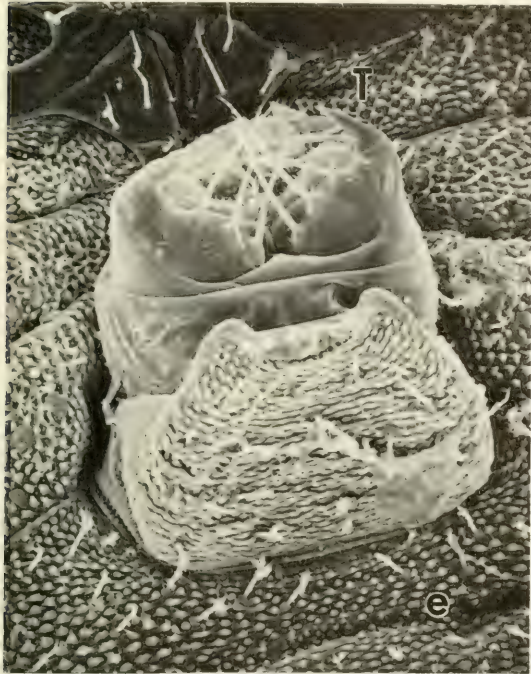
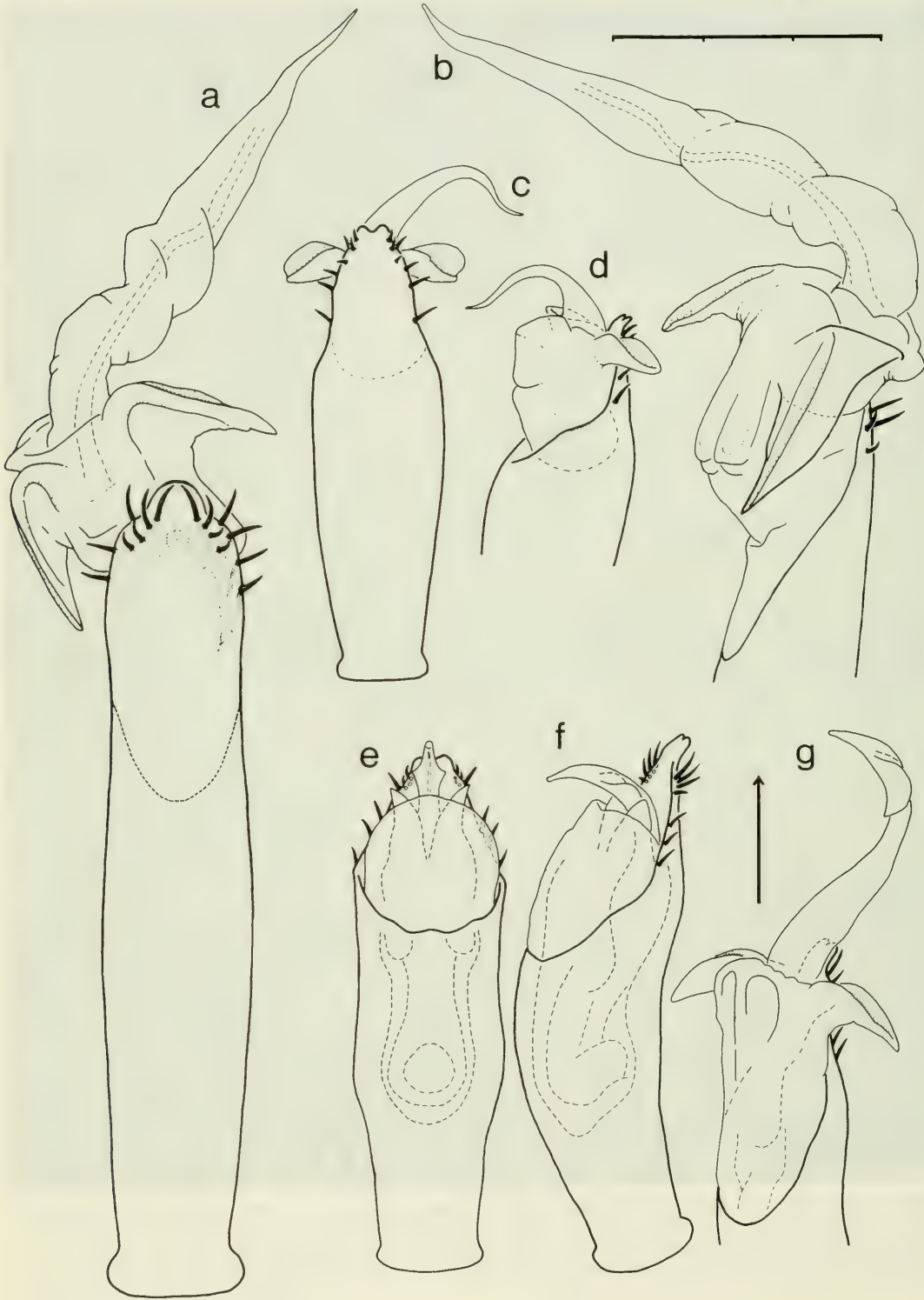


FIGURE 5. *Calicina*, ovipositors. (a) *C. mariposa*, lateral view (270 $\times$). (b) *C. mariposa*, close-up of lateral surface showing microspines (2,700 $\times$). (c) *C. mariposa*, apical view (390 $\times$). (d) *C. topanga*, lateral view showing subapical setae (S) (230 $\times$). (e) *C. palapraeputia*, ventral view showing apical tooth (T) (170 $\times$). (f) *C. palapraeputia*, apical view showing microspines and anterior margin of genital operculum (230 $\times$). (g) *C. serpentina*, lateral view showing apical tooth (310 $\times$). (h) *C. serpentina*, apical view showing microspines (390 $\times$).





8. Dorsal process with apical bifurcation (Fig. 12) *minor* subgroup
- Dorsal process with apical lobes 9
9. Dorsal process with 5 apical lobes; ventral plate with at most 4 pairs of lateral setae (Fig. 13, 14) *serpentina* subgroup
- Dorsal process with at most 4 apical lobes; ventral plate with 5 to 8 pairs of lateral setae (Fig. 15) *sequoia* subgroup

THE *MARIPOSA* SPECIES GROUP
(The *mariposa* Subgroup)

DIAGNOSIS.—Members of the *mariposa* group may be recognized by their simple genitalia. The glans consists of a stylus and a basal segment bearing collar lobes and lacks additional sclerites. The ovipositor contains the full complement of 12 apical and 3 pairs of subapical setae. The dorsal grooves on the collar lobes are synapomorphic for the group. The three species belonging to this group are all summer-active forest dwellers.

DISTRIBUTION.—The *mariposa* group is found only in the central Sierra Nevada in Yosemite National Park at elevations of 1,200–2,000 m.

***Calicina mariposa* (Briggs, 1968),
new combination**

(Fig. 2, 3a, c, 4a, 5a–c, 6a, b, 16a, b)

Sitalcina mariposa Briggs, 1968:31.

DIAGNOSIS.—This species differs from other members of the group in having a high tarsal count of 3-5-5-5; males lack an apical notch on the ventral plate of the penis.

ADDITIONAL DESCRIPTION.—Carapace with 6–8 pairs of anterior tubercles. Penis large; ventral plate apically entire and with 8 pairs of marginal setae; collar lobes pointed and pocketlike; stylus long and sinuous. Ovipositor with 12 apical setae and 3 pairs of lateral, subapical setae; microspines on apical and lateral surfaces.

TYPE SPECIMENS.—Male holotype, female allotype, and three paratypes (one male, two females), under logs in a giant sequoia grove at Mariposa Big Trees, Yosemite National Park, Mariposa County, 28 July 1967, TSB and KH.

SPECIMENS EXAMINED.—Four males, 12 females.

NEW RECORDS.—**MARIPOSA COUNTY:** Mariposa Big Trees, 26 July 1984 (TSB, SK, GT); **TUOLUMNE COUNTY:** Yosemite National Park: Tioga Pass Road, June 1970 (TSB); 9.2 km E Crane Flat Junction, 27 July 1984 (TSB, SK, GT); Wawona Camp, 17 Sep. 1941 (WI; AMNH collection).

NATURAL HISTORY.—Known from sequoia and yellow pine forests; collected from June to September.

***Calicina yosemitensis* (Briggs, 1968),
new combination**

(Fig. 6e–g)

Sitalcina yosemitensis Briggs, 1968:31.

DIAGNOSIS.—Males of this species have a glans with a uniquely modified stylus tip; females may be separated from other group members in having an ovipositor with only 1 pair of subapical setae.

ADDITIONAL DESCRIPTION.—Carapace with 4–8 pairs of anterior tubercles. Penis medium-sized; ventral plate with apical notch and 7 pairs of lateral setae; collar lobes small, pointed, apically grooved; stylus tip with lateral expansions. Ovipositor as in *mariposa* but with only 1 pair of subapical setae.

TYPE SPECIMENS.—Male holotype, female allotype, and three paratypes (two males, one female), under fallen bark in coniferous forest 5.0 mi (8.0 km) E Crane Flat Ranger Station, Yosemite National Park, Tuolumne County, 28 July 1967, TSB and AL.

SPECIMENS EXAMINED.—Five males, three females.

NEW RECORD.—**TUOLUMNE COUNTY:** Yosemite National Park: 3.8 mi (6.1 km) NE Crane Flat Ranger Station, 21 July 1968 (TSB, MW, GL).

***Calicina conifera* Ubick and Briggs,
new species**

(Fig. 6c, d)

DIAGNOSIS.—This species differs from others in the *mariposa* group by its small size, pale coloration, and absence of retina.

ETYMOLOGY.—The specific name refers to the coniferous biome in which this species lives.

DESCRIPTION.—Color yellowish orange. Car-

FIGURE 6. Male genitalia of the *mariposa* group. (a, b) *C. mariposa* (Crane Flat Junction), ventral and lateral views. (c, d) *C. conifera* (holotype), ventral and lateral views. (e–g) *C. yosemitensis*. (e, f) Dorsal and lateral views showing retracted glans (paratopotype). (g) Dorsolateral view showing expanded glans, arrow indicates movement of glans during expansion (3.8 mi NE Crane Flat). Note: Unless otherwise indicated, the scale bar for these and all subsequent genitalic drawings equals 0.30 mm, and all drawings are of fully expanded glands.

apace with 3 or 4 pairs of anterior tubercles. Retina absent, lens present. Tarsal count 3-4-4-5.

Male: Total body length, 1.20. Scute length, 0.80. Scute width, 0.88. Eye tubercle length, 0.12. Eye tubercle width, 0.16. Leg II length, 2.13. Palpal tarsus with dorsal spur. Penis small; ventral plate apically notched and with 7 pairs of marginal setae; collar lobes small, rounded and apically grooved; stylus uniformly tapering and sinuous.

Female: Total body length, 1.00. Scute length, 0.63. Scute width, 0.71. Eye tubercle length, 0.13. Eye tubercle width, 0.11. Ovipositor as in *mariposa* but with two pairs of subapical setae.

TYPE SPECIMENS.—Male holotype and two female paratypes, under fallen bark in a mixed coniferous forest at 1.8 km E Crane Flat Junction, Tuolumne County, 29 July 1984, TSB, SK, and GT.

SPECIMENS EXAMINED.—Only the type series.

THE *DIGITA* SPECIES GROUP

DIAGNOSIS.—The parastyli on the glans penis is the presumed synapomorphy for this group.

The *digita* Subgroup

DIAGNOSIS.—The *digita* subgroup is distinguished from all others by the unique male genitalia: the ventral plate is arrow-shaped and the glans bears a pair of slender, ventral parastyli. Males have a large dorsal spur on the palpal tarsus.

DISTRIBUTION.—Middle elevation Sierra Nevada from Amador south to Tulare counties.

Calicina digita (Briggs and Hom, 1967), new combination

(Fig. 7a-d, 16c, d)

Sitalcina digitus Briggs and Hom, 1967:51. Briggs, 1968:20.

DIAGNOSIS.—This species is easily distinguished from the other in its subgroup by a higher tarsal count of 3-5-5-5.

ADDITIONAL DESCRIPTION.—Carapace with 6 or 7 pairs of anterior tubercles. Glans with a pair of short, scalelike parastyli and long, sinuous stylus. Ventral plate with 7 pairs of setae. Ovipositor similar to that of *mariposa* but with lower density of microspines and with 2 or 3 pairs of subapical setae.

TYPE SPECIMENS.—Male holotype, female allotype, and 20 paratypes (12 males, eight females), under fallen bark at 2.2

mi (3.5 km) S Giant Forest, Sequoia National Park, Tulare County, 15 May 1966, TSB and KH.

SPECIMENS EXAMINED.—Twenty-seven males, 22 females.

NEW RECORDS.—MARIPOSA COUNTY: 3 mi (5 km) E Briceburg, 6 Feb. 1954 (ROS; AMNH collection); Merced River, N Fork near Main Fork, 31 Mar. 1983 (TSB, SO). FRESNO COUNTY: Saturday Cave, near Boyden Cave, 15 May 1966 (TSB); Big Creek, 7 Aug. 1956 (ROS; UCB collection). TULARE COUNTY: Sequoia National Park: 0.9 mi (1.4 km) S Giant Forest Village, 17 Aug. 1984 (TSB, VFL, DU); 4 mi (6.4 km) N Hospital Campground, 13 Feb. 1967 (JSB, MG).

NATURAL HISTORY.—Found in a variety of biomes, including forests (giant sequoia-yellow pine forest, oak woodland) and grassland, and collected throughout the year. There is one collection from a cave.

REMARKS.—The disjunct populations do not appear to differ in reproductive or somatic characters.

Calicina sierra (Briggs and Hom, 1967), new combination

(Fig. 7e-g)

Sitalcina sierra Briggs and Hom, 1967:49.

Sitalcina sierra sierra Briggs and Hom. Briggs, 1968:20.

DIAGNOSIS.—*Calicina sierra*, a pedomorphic species, is most readily distinguished from *digita* by its low tarsal count of 3-4-4-4.

ADDITIONAL DESCRIPTION.—Carapace with 3 or 4 pairs of anterior tubercles. Penis similar to, but smaller than, that of *digita*. Ovipositor as in *mariposa*.

JUVENILES.—One of the two juveniles is an early instar (from Scat Cave) having a tarsal count of 1-1-2-2, the other is a penultimate (McLean's Cave area, 2 Nov. 1975) just prior to moulting. Both instars lack anterior tubercles. The late instar has several robust spines on each of the free tergites; the early instar has only one pair of such spines restricted to tergite VII. The eyes of both instars are well developed, as in adults.

TYPE SPECIMENS.—Male holotype, female allotype, and five paratypes (three males, two females), 6.2 mi (10.0 km) N Mercer Caverns, Sheep Ranch Road, Calaveras County, 26 Mar. 1966, TSB and KH.

SPECIMENS EXAMINED.—Forty-three males, 30 females, two juveniles.

NEW RECORDS.—CALAVERAS COUNTY: Music Hall Cave, 7.2 km ESE Angel's Camp, 18 May 1977 (AGG, SW, MM, NB); Carlow's Bat Cavern, 7 km SE Angel's Camp, 25 May 1977 (DB, SW, AGG); Scat Cave, 4 mi (6.4 km) W Columbia, 26 Mar. 1979 (BM, SW); unnamed cave, Peruvian Gulch, 2 mi (3.2 km) NW Columbia, 10 May 1980 (DU); Speleogen Cave, 7 km SE Angel's Camp, 20 Apr. 1980 (TSB, DU). TUOLUMNE COUNTY: Lower van Trump Mine, Fox Gulch,

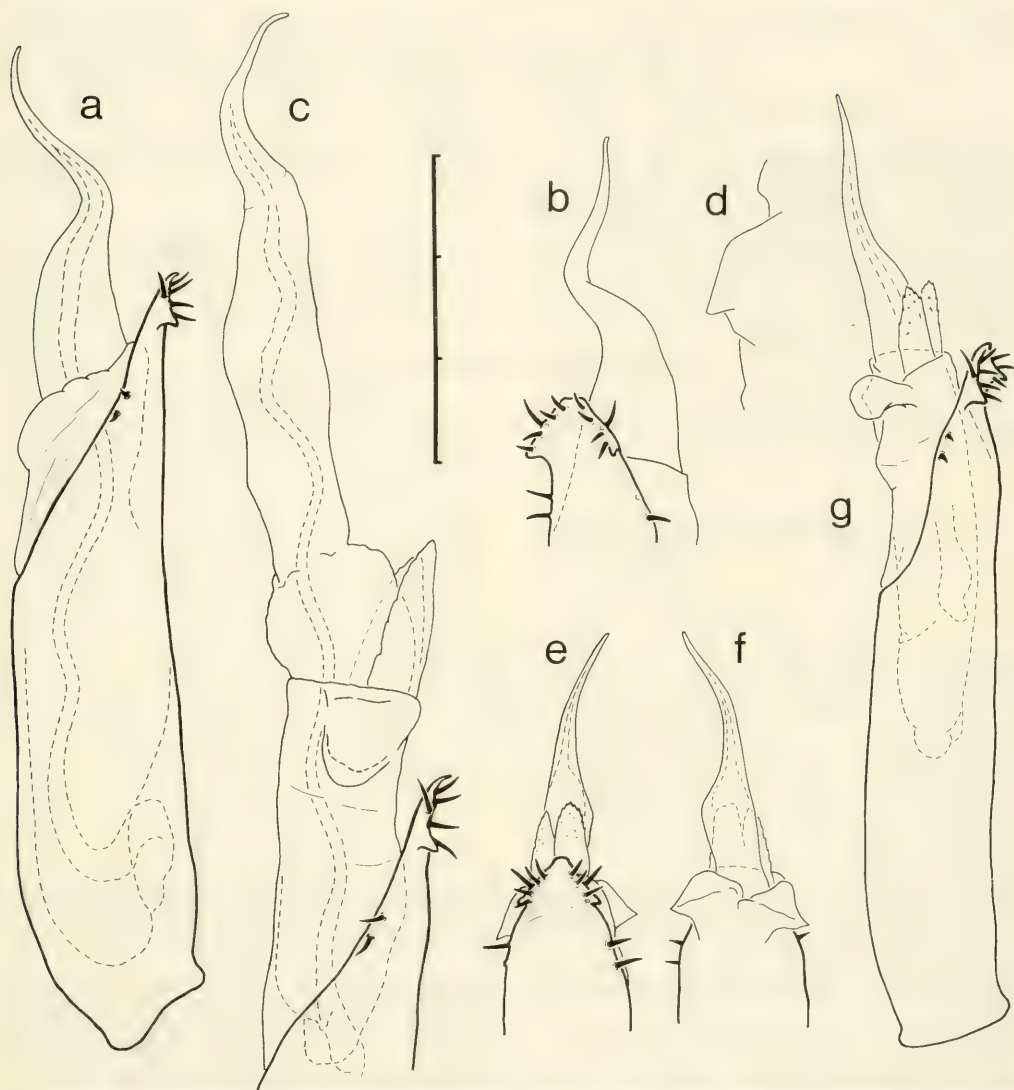


FIGURE 7. Male genitalia of the *digita* subgroup. (a–d) *C. digita*. (a, b) Lateral and subventral views showing retracted glans (Merced River). (c, d) Lateral view of expanded glans and dorsal view of left collar lobe (Giant Forest). (e–g) *C. sierra* (McLean's Cave area), ventral, dorsal, and lateral views.

23 Sep. 1975 (TSB, RL); Porcupine Skull Cave, 2 mi (3.2 km) N Columbia, 11 Feb. 1979 (DCR, SW); 2.5 mi (4 km) NW Columbia, 2 Feb. 1979 (DCR, SW); S Fork Stanislaus River at Marble Quarry Road, 5 Mar. 1981 (DU); 2.5 mi (4 km) N Columbia, McLean's Cave area, 2 Nov. 1975 (TSB, RL), 2 Apr. 1979 (DCR, BM, SW).

DISTRIBUTION.—Known from Amador, Calaveras, and Tuolumne counties.

NATURAL HISTORY.—Found in digger pine-oak forests during the winter and spring months (November–April). *C. sierra* is also known from caves, where it is active throughout the year,

although it has never been collected in association with the sympatric, cavernicolous species of *Banksula*. In an extensive survey of the Calaveras Formation caves, *Banksula* was recorded from more than 30 caves and *C. sierra* from six different ones (Briggs and Ubick 1981).

The *kaweahensis* Subgroup

DIAGNOSIS.—Males of the *kaweahensis* subgroup are unique in having a penis with ornate, lateral parastyli.

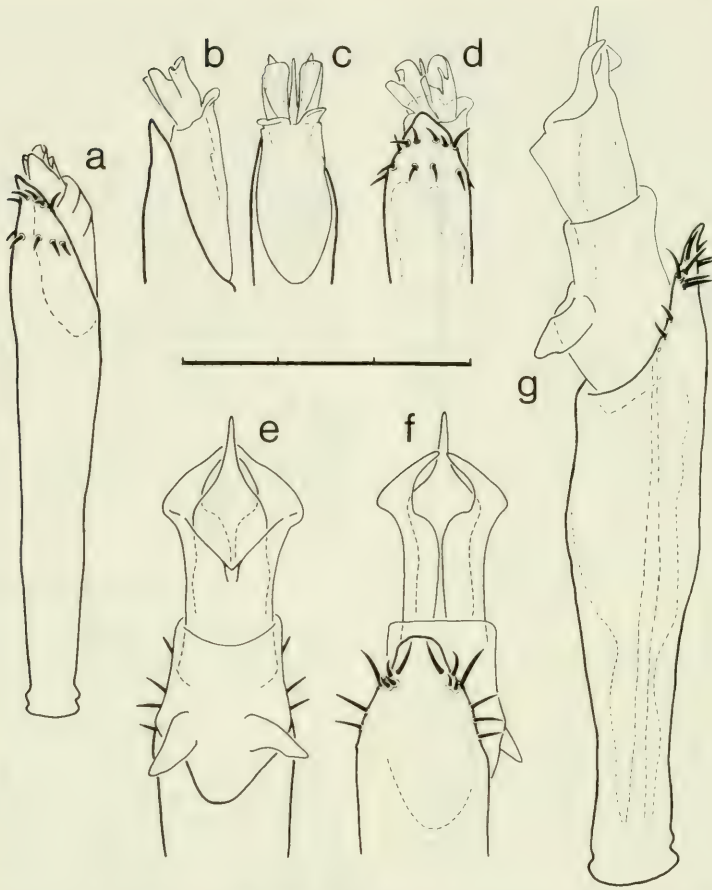


FIGURE 8. Male genitalia of the *kaweahensis* subgroup. (a-d) *C. galena*. (a) Sublateral view showing retracted glans (holotype). (b-d) Lateral, dorsal, and ventral views (paratopotype). (e-g) *C. kaweahensis* (Rocky Hill), dorsal, ventral, and lateral views.

DISTRIBUTION.—Known only from Tulare County.

***Calicina kaweahensis* (Briggs and Hom, 1966), new combination**
(Fig. 8e-g)

Sitalcina kaweahensis Briggs and Hom, 1966:266. Briggs, 1968: 22.

DIAGNOSIS.—This species may be distinguished by the combination of large size (body length greater than 1.4 mm) and a tarsal count of 3-5-4-5. Males have a glans with uniquely modified parastyli.

ADDITIONAL DESCRIPTION.—Carapace with 4 pairs of anterior tubercles. Penis with collar lobes in basal position; parastyli dorsally fused and

apically attenuated; stylus straight and basally enlarged; ventral plate with 8 pairs of marginal setae. Ovipositor as in *mariposa* but with 2 pairs of subapical setae and with a pair of large apical teeth; microspines on entire distal segment but sparse on the ventral surface.

TYPE SPECIMENS.—Female holotype, male allotype, and two paratypes (damaged), under granitic rocks at 0.3 mi (0.5 km) N Junction of Woodlake-Lemoncove Road on road to Badger, Tulare County, 26 Nov. 1965, TSB and VFL.

SPECIMENS EXAMINED.—Seventeen males, 11 females, four specimens of undetermined sex (damaged).

NEW RECORDS.—TULARE COUNTY: 0.3 mi (0.5 km) N junction Woodlake-Lemoncove Road, 18 Dec. 1965 (KH); near Lake Kaweah Offices on Hwy 198, 14 May 1966 (TSB); near Kaweah Dam on Hwy 198, 26 Nov. 1965 (VFL); 2.1 mi (3.4 km) E Rocky Hill Town, 19 Dec. 1966 (TSB, KH); 1.4 mi (2.3 km) E Rocky Hill Town, 22 Jan. 1967 (TSB, KH, AKSJ); Yokohl Valley, near Lindsay, Feb. 1971 (TSB); Three Rivers, Nov. 1967 (TSB).

NATURAL HISTORY.—Known from oak woodland biomes and collected throughout the winter and spring months (November–May).

***Calicina galena* Ubick and Briggs,**
new species

(Fig. 8a–d)

DIAGNOSIS.—Males of this species differ from all others by the ornately scrolled parastyli and the unique transverse rows of setae on the ventral plate.

ETYMOLOGY.—The specific name refers to the type locality and is a name in apposition.

DESCRIPTION.—Carapace with 1 pair of anterior tubercles. Eyes present. Tarsal count 3-5-5-5 or 3-5-4-5.

Male: Total body length, 1.17. Scute length, 0.79. Scute width, 0.72. Eye tubercle length, 0.17. Eye tubercle width, 0.12. Leg II length, 1.94. Color yellowish orange. Palpal tarsus without dorsal spur. Penis with ventral plate bearing 6 pairs of setae arranged in two transverse rows; collar lobes reduced to small flaps; parastyli intricately scrolled; stylus short and spinelike.

Female: Total body length: 1.01. Scute length, 0.69. Scute width, 0.78. Eye tubercle length, 0.13. Eye tubercle width, 0.12. Color orange. Ovipositor as in *mariposa*.

VARIATION.—Some specimens from the Johnsondale localities have the basal tarsomeres of tarsus III fused, giving a tarsal count of 3-5-4-5.

JUVENILES.—The single known juvenile is very pale, has a tarsal count of 3-5-4-5, and has well developed eyes. As in adults, one pair of anterior tubercles is present, and the abdominal tergites lack robust setae.

TYPE SPECIMENS.—Male holotype and 11 paratypes (two males, eight females, one juvenile), Galena Creek, Mountain Home State Forest, Tulare County, 4 Sep. 1967, TSB. Ten paratypes (seven males, three females), 2.25 mi (3.6 km) W Johnsondale, Tulare County, 1,600 m, 2 July 1988, TSB and DU. Nineteen paratypes (12 males, seven females), Double Bunk Meadows, 3.5 air mi (5.6 km) SW Johnsondale, Tulare County, 1,850 m, 3 July 1988, TSB and DU.

SPECIMENS EXAMINED.—Only the type series.

NATURAL HISTORY.—The original series was collected beneath granite rocks in a giant sequoia forest. The recent collections are from mixed coniferous forests; specimens were collected beneath and within decaying logs, large slabs of fallen bark, and dense mats of duff. The popu-

lation at 3.6 km W Johnsondale is sympatric with a species of *Sitalcina*.

The *topanga* Subgroup

DIAGNOSIS.—This subgroup is distinguished from all others by several unique male genital characters: apex of ventral plate attenuated and armed with two pairs of strong setae; stylus straight and elongated, somewhat flattened; parastyli short, hornlike in shape and dorsally situated; and collar lobes small and covered with minute tubercles.

DISTRIBUTION.—Members of this subgroup occur in the southern Coast Ranges and Tehachapi Mountains, the southernmost distribution of the genus.

***Calicina topanga* (Briggs, 1968),**
new combination

(Fig. 5d, 9c, d)

Sitalcina topanga Briggs, 1968:25.

DIAGNOSIS.—This species may be distinguished from others in the subgroup by its high tarsal count of 3-5-5-5.

ADDITIONAL DESCRIPTION.—Carapace with 2 or 3 pairs of anterior tubercles. Penis with ventral plate attenuated and bearing 7 pairs of setae, of which four apical ones are enlarged; collar lobes earlike lateral projections with microspines; parastyli dorsal, short and hornlike; stylus long and straight, somewhat flattened. Ovipositor as in *mariposa* but with 2–4 pairs of subapical setae (one specimen with 9 setae).

TYPE SPECIMENS.—Male holotype, female allotype, and four paratypes (two males, two females), under sandstone in a dense oak forest at 3.3 mi (5.3 km) N Topanga Beach in Topanga Canyon, Los Angeles County, 7 Apr. 1966, TSB, KH, and VFL.

SPECIMENS EXAMINED.—Thirty-eight males, 32 females, one specimen of undetermined sex.

NEW RECORDS.—SANTA BARBARA COUNTY: Santa Ynez Mountains, Cold Springs, 19 Dec. 1967 (TSB, AKSJ). Santa Cruz Island: canyon N UCSB Field Station, 19 Dec. 1967 (TSB, KH, AKSJ), 21 Dec. 1967 (TSB); 0.1 mi (0.2 km) SW UCSB Field Station, 20 Dec. 1967 (AKSJ); Cañada del Puerto, Prisoners Harbor, 21 Dec. 1967 (KH, AKSJ); Raven's Wood Canyon, 22 Dec. 1967 (TSB); Cristi Pines, 19–22 Dec. 1967 (TSB, KH, AKSJ).

NATURAL HISTORY.—Known from both closed and open forests (broadleaf evergreen, digger pine-oak, and oak woodland), and collected during the winter and spring months (December–April).

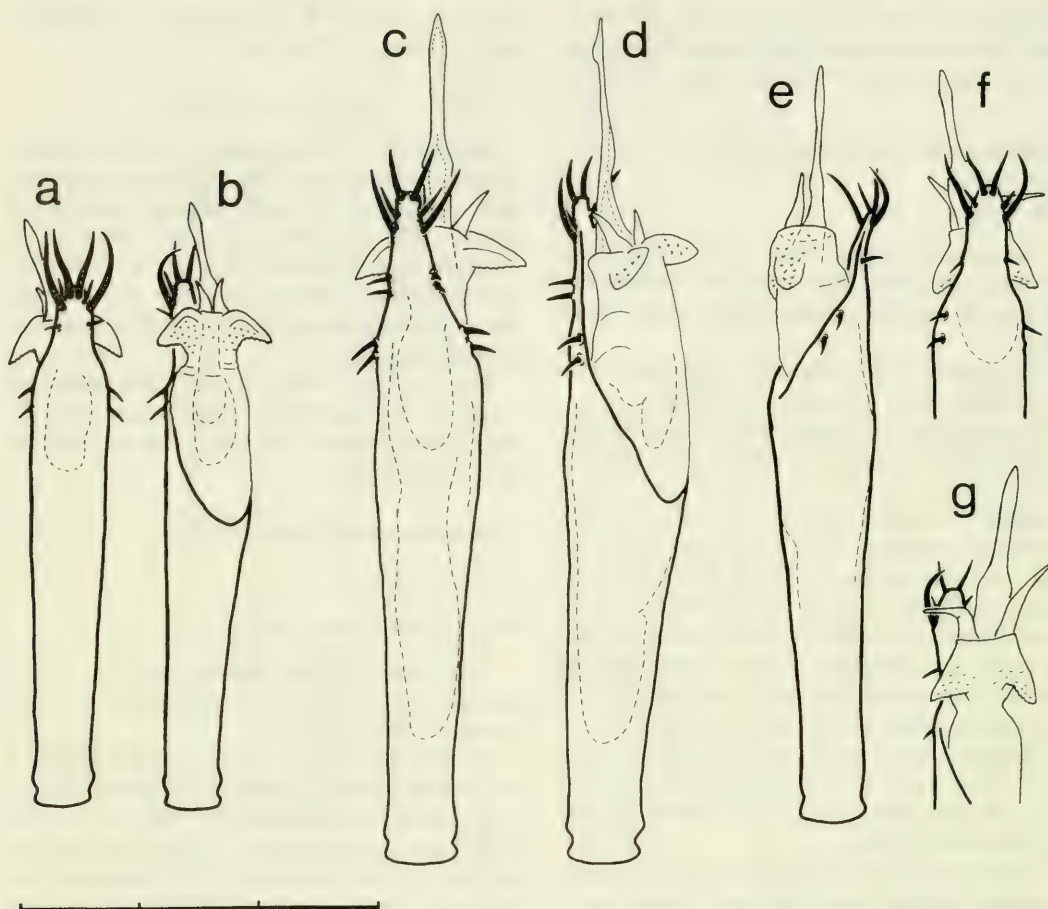


FIGURE 9. Male genitalia of the *topanga* subgroup. (a, b) *C. morroensis* (Madonna Inn), ventral and subdorsal views. (c, d) *C. topanga* (Santa Cruz Island), subventral and lateral views. (e-g) *C. keeneae* (holotype), lateral, ventral, and dorsal views.

REMARKS: The mainland and island populations of *topanga* appear similar in both genitalic and somatic characters.

Calicina keeneae (Briggs, 1968),
new combination
(Fig. 9e, f)

Sitalcina keeneae Briggs, 1968:25.

DIAGNOSIS.—This species is distinguished from others in its group by its tarsal count, 3-4-4-5.

ADDITIONAL DESCRIPTION.—Carapace with 2 or 3 pairs of anterior tubercles. Penis similar to but smaller than that of *topanga*; ventral plate with 6 pairs of lateral setae. Ovipositor as in *mariposa* but with 4 pairs of subapical setae and with a lower density of microspines.

TYPE SPECIMENS.—Male holotype and female allotype, under granite in moist oak grassland at 3.2 mi (5.1 km) NW Keene, Kern County, 19 Mar. 1967, VFL.

SPECIMENS EXAMINED.—Only the type series.

Calicina morroensis (Briggs, 1968),
new combination
(Fig. 9a, b)

Sitalcina morroensis Briggs, 1968:26.

DIAGNOSIS.—This paedomorphic species differs from others in the group by the combination of low tarsal count of 3-4-4-4 and degenerate eyes (lacking retina and sometimes cornea).

ADDITIONAL DESCRIPTION.—Carapace with 1 pair of anterior tubercles. Penis typical for the group; ventral plate with strong apical setae and 6 pairs of lateral setae; stylus broad and flat,

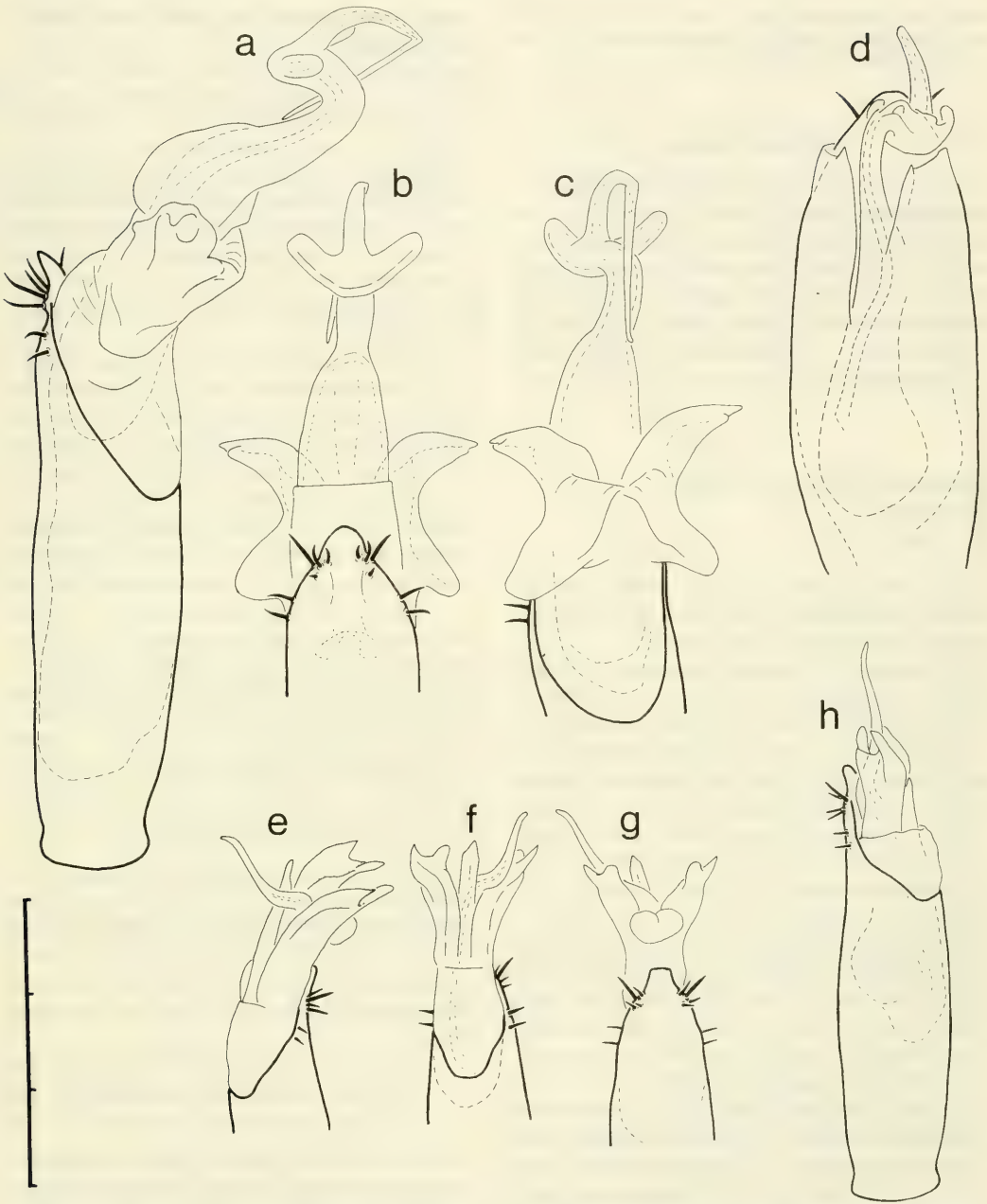


FIGURE 10. Male genitalia of the *arida* subgroup. (a-d) *C. cloughensis*. (a-c) Lateral, ventral, and dorsal views (topotype). (d) Dorsal view of slide-mounted specimen showing retracted glans (holotype). (e-h) *C. arida*. (e-g) Lateral, dorsal, and ventral views (holotype). (h) Sublateral view showing retracted glans (paratopotype).

parastyli very small. Ovipositor similar to that of *mariposa* but with 3 pairs of strongly reduced subapical setae and with sparse distribution of microspines.

TYPE SPECIMENS. — Male holotype and female allotype, under serpentine in marshy grassland at 0.8 mi (1.3 km) N Morro Bay, San Luis Obispo County, 2 Mar. 1967, VFL.

SPECIMENS EXAMINED. — Twenty-nine males, 25 females.

NEW RECORDS. — SAN LUIS OBISPO COUNTY: San Luis

Obispo, behind Madonna Inn, 22 Mar. 1970 (TSB, GL); 2.4 mi (3.9 km) NW San Simeon in serpentine grassland, 13 Feb. 1987 (TSB, VFL).

The *arida* Subgroup

DIAGNOSIS.—Members of this subgroup are distinguished from all other species by their unique glans penis: the stylus is strongly sinuous and the collar lobes are greatly enlarged. Males also lack spurs on their palpal tarsi but have enlarged mesobasal, spine-bearing tubercles.

DISTRIBUTION.—Known from a single locality in San Benito County and a cave in Tulare County.

Calicina arida Ubick and Briggs, new species

(Fig. 10e-h)

DIAGNOSIS.—Males of this paedomorphic species are unique in the genus in having the parastyli represented by a single rod.

ETYMOLOGY.—The specific name is a Latin adjective meaning dry, and refers to the climatic conditions in the vicinity of the type locality.

DESCRIPTION.—Color yellowish orange. Carapace with 1 pair of anterior tubercles. Retina absent, cornea present. Tarsal count 3-4-4-4.

Male: Total body length, 0.80. Scute length, 0.57. Scute width, 0.56. Eye tubercle length, 0.10. Eye tubercle width, 0.13. Leg II length, 1.65. Palpal tarsus without dorsal spur but with enlarged mesobasal spine-bearing tubercle. Penis relatively stout; ventral plate with slight apical attenuation and 6 pairs of setae; collar lobes greatly enlarged and apically directed; parastyli represented by a single, dorsal rod; stylus strongly sinuous and dorsally directed.

Female: Total body length, 0.73. Scute length, 0.50. Scute width, 0.53. Eye tubercle length, 0.06. Eye tubercle width, 0.08. Ovipositor with 12 apical setae, with 3 pairs of subapical setae and with a pair of short apical teeth; microspines sparsely distributed apically and laterally.

TYPE SPECIMENS.—Male holotype and 18 paratypes (nine males, nine females), under serpentine rocks in an oak gully at Panoche Road, 12.7 mi (20.4 km) SE Paicines, San Benito County, 1 Dec. 1984, TSB, VFL, and DU. One male paratype, 1 Dec. 1971, KH. Two paratypes (male, female) deposited at AMNH collection.

SPECIMENS EXAMINED.—Eleven males, 10 females.

Calicina cloughensis (Briggs and Hom, 1967), new combination

(Fig. 10a-d)

Sitalcina cloughensis Briggs and Hom, 1967:52. Briggs, 1968: 23.

DIAGNOSIS.—This species is the only troglotibitic *Calicina* and is recognized by its pale coloration, complete loss of eyes (cornea as well as retina), and a high tarsal count (3-5-5-5). Furthermore, males of *cloughensis* have bilobed collar lobes and a unique stylus bearing a median enlargement.

ADDITIONAL DESCRIPTION.—Carapace with 1 pair of anterior tubercles. Penis with ventral plate bearing 6 pairs of lateral setae; collar lobes divided into apical and basal portions; stylus long and sinuous, with crescent-shaped enlargement at midlength, and with apical extension. Ovipositor with 12 apical setae (nine in one specimen) and 2 or 3 pairs of subapical setae; microspines sparsely distributed on lateral surface.

JUVENILES.—Two of the paratypes are early instar juveniles having tarsal counts of 1-2-2-2 and completely lacking eyes. Both lack anterior tubercles but have robust spines on the free tergites (adults have normal setae).

TYPE SPECIMENS.—Male holotype, female allotype, and six paratypes (male, three females, two juveniles), in Ladder Room of Clough Cave at South Fork Ranger Station 1,070 m (3,500 ft), Sequoia National Park, Tulare County, 14 May 1966, TSB, VFL, and KH.

SPECIMENS EXAMINED.—Four males, nine females, two juveniles.

NEW RECORDS.—TULARE COUNTY: Clough Cave, 18 Apr. 1979 (SW, EVI), 31 Aug. 1986 (TSB, KH, AKSJ).

REMARKS.—The stylus of the holotype male lacks the apical extension found in other specimens.

THE *PALAPRAEPUTIA* SPECIES GROUP (The *palapraeputia* Subgroup)

DIAGNOSIS.—The single species representing this group has unique male genitalia: glans of penis three segmented with middle segment bearing a pair of hornlike collar lobes.

DISTRIBUTION.—Found only in Fresno County.

Calicina palapraeputia (Briggs, 1968), new combination

(Fig. 5e, f, 11, 16e, f)

Sitalcina palapraeputia Briggs, 1968:29.

DIAGNOSIS.—Same as for group.

ADDITIONAL DESCRIPTION.—Carapace with 2 or 3 pairs of anterior tubercles. Genital operculum with concave anterior margin. Penis with ventral plate truncate, apically elongated and armed with 7 pairs of setae; glans with two collars; collar lobes raptorial; stylus stout. Ovipositor with short distal segment, with 7 pairs of apical setae, and with a pair of large apical teeth; microspines present only at apex.

TYPE SPECIMENS.—Male holotype, female allotype, and six paratypes (three males, three females), under serpentine rocks in open grassland at 7 mi (11 km) NE Piedra, Fresno County, 21 Jan. 1967, TSB and KH.

SPECIMENS EXAMINED.—Fifteen males, 10 females.

NEW RECORDS.—FRESNO COUNTY: 10.2 mi (16.4 km) SW Trimmer, 27 Jan. 1968 (KH, JG); 8.7 mi (14 km) SW Trimmer, 27 Jan. 1968 (TSB, KH); 5.3 mi (8.5 km) SW Trimmer, 27 Jan. 1968 (TSB).

NATURAL HISTORY.—Found beneath serpentine and granite rocks in oak woodland and grassland biomes.

THE *SERPENTINEA* SPECIES GROUP

DIAGNOSIS.—Males of this group have a dorsal process on the glans penis. Females differ from those in the *digita* and *mariposa* groups in having an ovipositor with only apical microspines.

The *minor* Subgroup

DIAGNOSIS.—The morphology of the penis, dorsal process with ventrally directed basal lobes but no apical lobes, is diagnostic for the subgroup.

DISTRIBUTION.—Known only from San Mateo County.

Calicina minor (Briggs and Hom, 1966), new combination
(Fig. 4c, 12)

Sitalcina minor Briggs and Hom, 1966:263. Briggs, 1968:27.

DIAGNOSIS.—This paedomorphic species is distinguished from all others by its unique glans penis: basal segment with transverse rows of small tubercles and dorsal process lacking apical lobes but with prominent basal lobes.

ADDITIONAL DESCRIPTION.—Carapace with at most 1 pair of anterior tubercles. Male palpal tarsus with enlarged mesobasal spine-bearing tubercle instead of spur. Penis with ventral plate apically produced and bearing 7 pairs of setae;

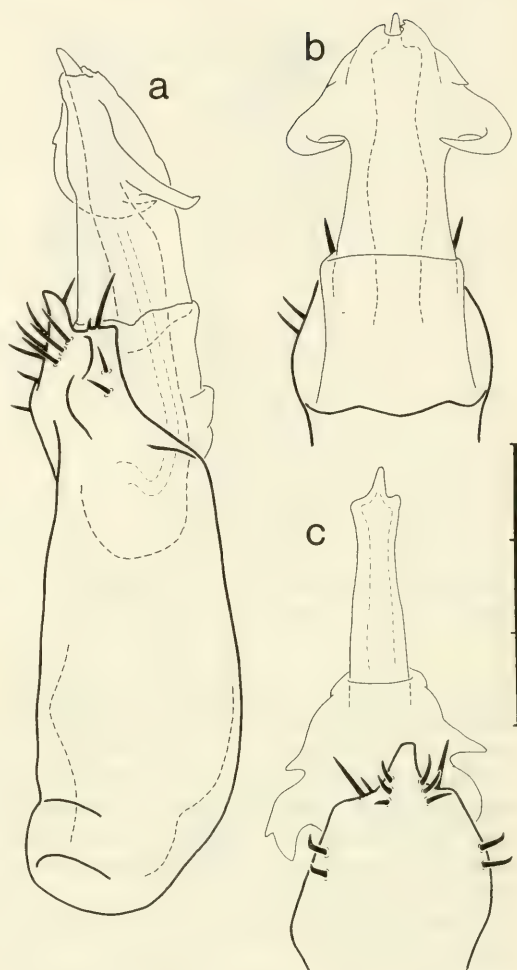


FIGURE 11. Male genitalia of *C. palapraeputia*. (a, b) Lateral and dorsal views showing partially expanded glans (5.3 mi SW Trimmer). (c) Ventral view showing fully expanded glans (10.2 mi SW Trimmer).

dorsal process apically bifurcate, with ventrally directed basal lobes; stylus straight and tapering, basally thickened. Ovipositor with 6 pairs of apical and 3 pairs of subapical setae; microspines restricted to apex.

TYPE SPECIMENS.—Female holotype, male allotype, and four paratypes (one male, three females), under serpentine rocks on grassland hillside at 0.75 mi (1.2 km) N Crystal Springs Dam on County Road No. 14, San Mateo County, 23 Jan. 1966, TSB and KH.

SPECIMENS EXAMINED.—Twenty males, 23 females.

NEW RECORDS.—SAN MATEO COUNTY: Edgewood Park, serpentine grassland on N half of park, 2 Jan. 1983 (TSB, VFL, DU); 6 Apr. 1986 (TSB, TO); 2 Jan. 1987 (TSB, VFL, DU); 24 Dec. 1987 (TSB, VFL, WES, DU).

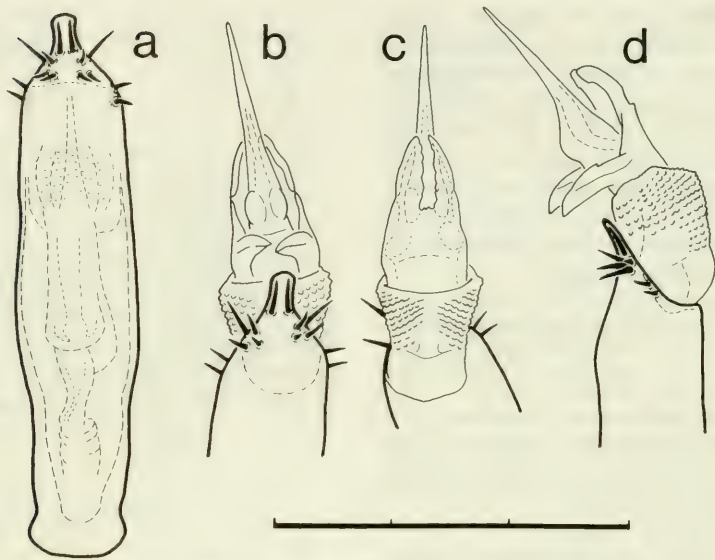


FIGURE 12. Male genitalia of *C. minor* (Edgewood Park). (a) Ventral view of penis shaft. (b-d) Ventral, dorsal, and lateral views.

DISTRIBUTION.—This species is presently known only from Edgewood Park. No specimens have been collected at the type locality (despite repeated attempts) since the completion of the adjacent highway. Also, the series of collections from Santa Clara County listed by Briggs and Hom (1966) represent an undescribed species belonging to a related genus.

NATURAL HISTORY.—All collections are from serpentine grassland.

The *serpentinea* Subgroup

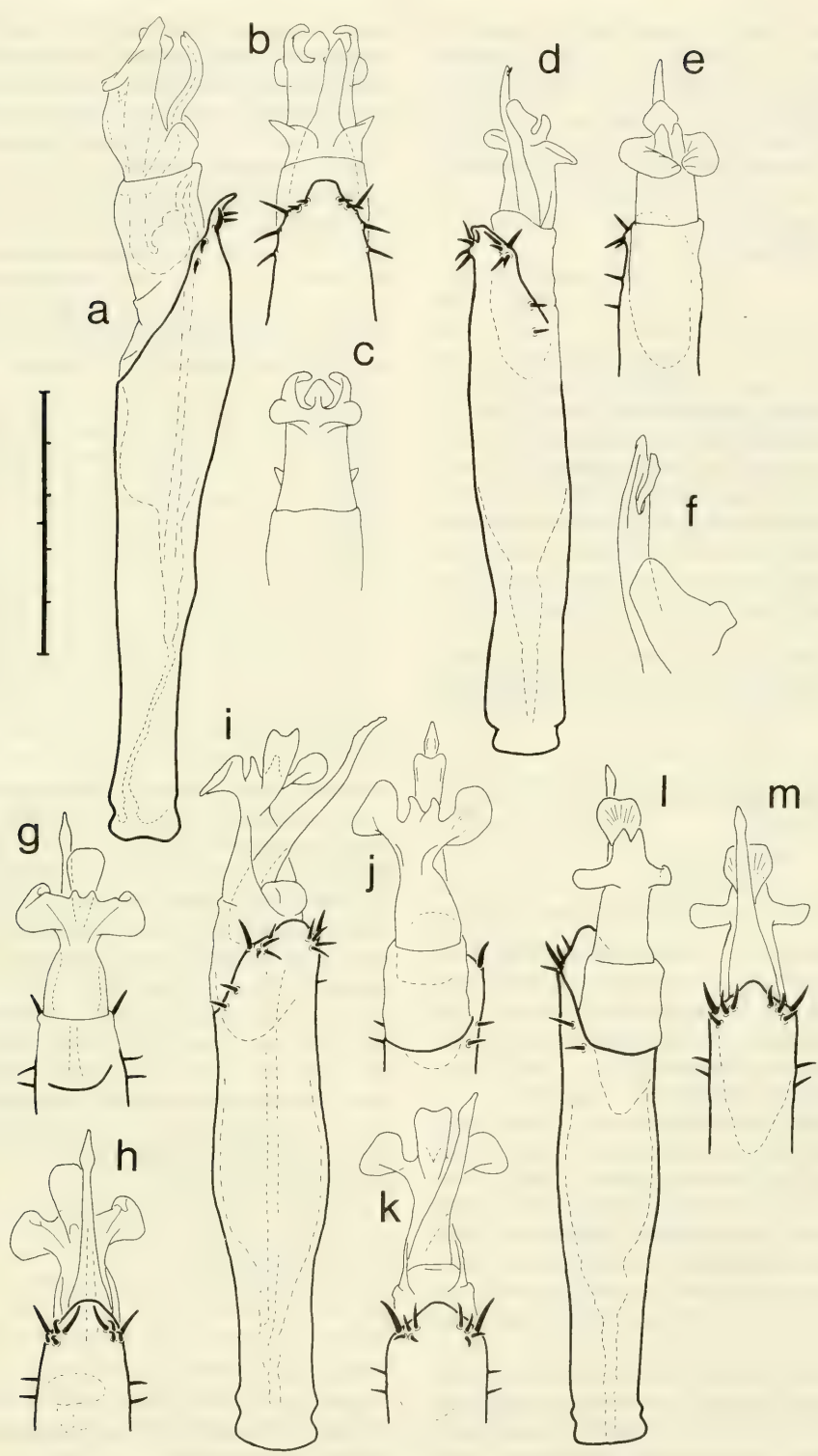
DIAGNOSIS.—This subgroup, the largest in *Calicina*, includes those species whose males have a glans with a ventral stylus and a dorsal process bearing five apical lobes. The palpal spur, when present, is small or vestigial.

DISTRIBUTION.—The subgroup has a disjunct distribution with two populations in the lower Sierra Nevada foothills and a third along the central and northern Coast Ranges.

Key to Males of the Species of the *serpentinea* Subgroup

- 1. Glans with a pair of basal lobes (Fig. 13a-c, 18) *pieдра*
- Glans without basal lobes (Fig. 13d-m, 14) 2
- 2. Stylus longer than dorsal process (Fig. 13d-m) 3
- Stylus shorter than dorsal process (Fig. 14) 5
- 3. Tarsal count 3-4-4-5 *serpentinea*
- Tarsal count 3-4-4-4 4
- 4. Dorsal process with lateral lobes as long as wide (Fig. 13d-f) *ensata*
- Dorsal process with lateral lobes longer than wide (Fig. 13l, m) *polina*
- 5. Body with dark maculations *macula*
- Body concolorous 6
- 6. Dorsal process with lateral lobes as long as wide (Fig. 14a-f) 7
- Dorsal process with lateral lobes longer than wide (Fig. 14j-l) 8

FIGURE 13. Male genitalia of the *serpentinea* subgroup. 1. (a-c) *C. pieдра* (holotype), lateral, ventral, and dorsal views. (d-f) *C. ensata* (Tollhouse). (d, e) Ventrolateral and dorsal views. (f) Dorsolateral view of stylus tip. (g-k) *C. serpentinea*. (g, h) Dorsal and ventral views (Monte Vista). (i-k) Ventrolateral, dorsal, and ventral views (San Felipe Road). (l, m) *C. polina* (Novato), dorsolateral and ventral views. (Scale bar equals 0.25 mm, except for "f" where it equals 0.10 mm.)



7. Median lobe of dorsal process apically notched (Fig. 14d-f) *basalta*
 - Median lobe of dorsal process apically pointed (Fig. 14a-c) *brevia*
 8. Tarsal count 3-4-4-5 *dimorphica*
 - Tarsal count 3-4-4-4 *mesaensis*

Calicina piedra (Briggs, 1968),
 new combination
 (Fig. 13a-c)

Sitalcina piedra Briggs, 1968:24.

DIAGNOSIS.—This species, the largest of the *serpentinea* group, is easily distinguished by the structure of the male genitalia: dorsal process of glans subequal in length to stylus, with a pair of basoventral lobes, and with small apical lobes.

ADDITIONAL DESCRIPTION.—Carapace with 2 or 3 pairs of anterior tubercles. Penis with ventral plate apically attenuated and with 5 pairs of lateral setae; stylus flat, broad, and sinuous. Ovipositor as in *minor* but without subapical setae.

TYPE SPECIMENS.—Male holotype, female allotype, and female paratype, under rocks in an oak grassland at 1.6 mi (2.6 km) SW Piedra, Fresno County, 21 Jan. 1967, TSB, KH, and AJ.

SPECIMENS EXAMINED.—Only the type series.

Calicina serpentinea (Briggs and Hom, 1966),
 new combination
 (Fig. 3b, 5g, h, 13g-k, 16g, h)

Sitalcina serpentinea Briggs and Hom, 1966:268. Briggs, 1968: 26.

DIAGNOSIS.—This species differs from others in its group by the combination of a tarsal count of 3-4-4-5 and structure of the male genitalia (stylus longer than the dorsal process and median lobe narrow and elongated).

ADDITIONAL DESCRIPTION.—Carapace with 2 or 3 pairs of anterior tubercles. Eyes variable, cornea present or absent. Tarsal spur of male palpi may be absent or extremely small. Penis with ventral plate bearing 7 pairs of setae; dorsal process with narrow median lobe (with or without an apical notch) and rounded lateral lobes. Ovipositor with apical microspines, with 6-8 pairs of apical setae, and with one pair of apical teeth.

VARIATION.—*Calicina serpentinea* is polymorphic with regard to several characters. Individuals from the three westernmost localities (dense forest biomes) lack corneas and tarsal

spurs, which are present in the remaining populations (grassland and oak woodland biomes). The female from Monte Vista lacks the paired apical teeth on the ovipositor. In individuals from Santa Clara and Contra Costa counties, the median lobe is apically entire (Fig. 13g, h), in others it is apically notched (Fig. 13i-k).

JUVENILES.—The two known juveniles, from Bob's Secret Cave, are middle instars having tarsal counts of 2-2-3-3. They lack anterior tubercles. As in adults from this locality, the eyes are completely reduced (lacking both retina and cornea) and the free tergites lack enlarged spines.

TYPE SPECIMENS.—Female holotype, male allotype, and six paratypes (two males, four females), under serpentine in marshy grassland along Silver Creek Road, 5 mi (8 km) SE Tully Road, San Jose, Santa Clara County, 27 Feb. 1966, TSB and CF.

SPECIMENS EXAMINED.—Fifty-one males, 38 females, two juveniles, seven specimens of undetermined sex.

NEW RECORDS.—SANTA CLARA COUNTY: Silver Creek Road, 3.6 mi (5.8 km) from San Felipe Road, 2 Jan. 1983 (TSB, VFL, DU); Silver Creek at San Felipe Reservoir, 27 Nov. 1966 (TSB, AKSJ); Monte Vista, near Permanente Quarry, 24 Mar. 1968 (TSB); Metcalf Road, 1.8 mi (2.9 km) N Hwy 101, 2 Jan. 1983 (TSB, VFL, DU). SANTA CRUZ COUNTY: Cave Gulch, Bob's Secret Cave, 6 May 1984 (TSB, VFL, DU); Cave Gulch, 18 June 1984 (TSB, DU). SAN BENITO COUNTY: Lone Tree Road, 8.6 mi (13.8 km) W Fairview Road, 27 Dec. 1984 (TSB, VFL, DU).

DISTRIBUTION.—Known from the southern Bay Area from San Mateo and Contra Costa to San Benito counties.

NATURAL HISTORY.—This wide-ranging species occurs in a variety of habitats; most commonly beneath serpentine in grassland and oak woodland biomes, but also from redwood, broadleaf evergreen, and digger pine-oak associations. There is also one collection from a cave. Most specimens were taken from under serpentine, but some were also collected beneath limestone and sandstone rocks, and fallen bark. While more commonly collected during the rainy season, this species is apparently active throughout the year in mesic refugia.

Calicina polina (Briggs, 1968),
 new combination
 (Fig. 13l, m)

Sitalcina polina Briggs, 1968:30.

DIAGNOSIS.—A unique dorsal process with a cordate median lobe and narrow lateral lobes distinguishes males of this paedomorphic species from all other species.

ADDITIONAL DESCRIPTION.—Carapace with 1 or 2 pairs of anterior tubercles. Penis with stylus longer than dorsal process; ventral plate with 6 pairs of setae. Ovipositor with 7 pairs of apical setae; microspines apical.

TYPE SPECIMENS.—Male holotype, female allotype, and three paratypes (two males, one female), under serpentine rocks in a moist grassland at El Polin Spring, Presidio, San Francisco County, 11 Dec. 1966, TSB.

SPECIMENS EXAMINED.—Forty-six males, 31 females, one specimen of undetermined sex.

NEW RECORDS.—SAN FRANCISCO COUNTY: Presidio Golf Course, 9 Nov. 1975 (TSB). MARIN COUNTY: 1 mi (1.6 km) NW Novato, 2 Apr. 1967 (TSB); Marin Dell Ranch, near Novato, 2 Jan. 1972 (TSB, AK); Novato, San Marin Drive, 7 Mar. 1982 (TSB, DU), 14 Mar. 1982 (DU); Novato, W of Burdell Mountain, 100 m (350 ft), 2 Jan. 1986 (TSB, DU); Novato, SW of Burdell Mountain, 170 m (550 ft), 2 Jan. 1986 (TSB, DU). SONOMA COUNTY: 2.5 mi (4 km) E Shellville, 2 Apr. 1967 (TSB); ALAMEDA COUNTY: Cull Canyon Road, 1 km N Crow Canyon Road, 22 Jan. 1984 (TSB, DU); Cull Canyon Road, 1.5 mi (2.4 km) N Crow Canyon Road, 22 Jan. 1984 (TSB, DU); Woolsey Canyon, Berkeley, 21 Dec. 1983 (TSB, VFL, DU); Redwood Road, 3.1 mi (5 km) N Castro Valley Road, 22 Jan. 1984 (TSB, DU); Chabot Reservoir at Lake Chabot Road, 6 Apr. 1982 (TSB, DU). CONTRA COSTA COUNTY: Wildcat Canyon Park near Hill Road, 30 Jan. 1984 (TSB), 14 July 1984 (TSB).

DISTRIBUTION.—This species is found in the northern part of the San Francisco Bay Region, from Sonoma south to San Francisco and Alameda counties.

NATURAL HISTORY.—The collections of *polina* west of San Francisco Bay (Sonoma, Marin, and San Francisco counties) are from serpentine grassland, whereas those from the East Bay are from beneath sandstone in oak forests.

***Calicina ensata* (Briggs, 1968),**
new combination

(Fig. 4d, 13d-f)

Sitalcina ensata Briggs, 1968:21.

DIAGNOSIS.—Males of this pedomorphic species may be distinguished from others in the subgroup in having a stylus which is longer than the dorsal process and has an apical prong.

ADDITIONAL DESCRIPTION.—Carapace with 2 or 3 pairs of anterior tubercles. Penis with ventral plate bearing 7 pairs of lateral setae; dorsal process with large lateral lobes; stylus long, tapering. Ovipositor with 12 apical setae and 3 pairs of subapical setae; microspines apical.

TYPE SPECIMENS.—Male holotype, female allotype, and 10 paratypes (eight males, two females), under rhyolite in an oak

woodland at 2.0 mi (3.2 km) NW Trimmer, Fresno County, 16 Apr. 1967, TSB.

SPECIMENS EXAMINED.—Sixteen males, seven females.

NEW RECORD.—FRESNO COUNTY: W entrance to Watts Valley, 28 Jan. 1968 (TSB).

NATURAL HISTORY.—This species is known from oak woodland and has been collected beneath granite, rhyolite, and serpentine rocks.

***Calicina macula* (Briggs, 1968),**
new combination

(Fig. 14g-i)

Sitalcina macula Briggs, 1968:23.

DIAGNOSIS.—This is the only *Calicina* with a dark marbled color pattern. Males of this pedomorphic species may also be distinguished by the proportions of the dorsal process lobes and in having enlarged mesoapical spine-bearing tubercles on male palpal tarsi.

ADDITIONAL DESCRIPTION.—Carapace with 2 pairs of anterior tubercles. Penis typical for the *serpentinea* group; dorsal process with notched median lobe; ventral plate with 7 pairs of lateral setae. Ovipositor with 12 apical and 3 pairs of subapical setae; microspines apical.

TYPE SPECIMENS.—Male holotype, female allotype, and nine paratypes (eight males, one female), under serpentine rocks in an oak grassland at 9 mi (14.5 km) SE Academy, Fresno County, 16 Apr. 1967, TSB.

SPECIMENS EXAMINED.—Only the type series.

***Calicina dimorphica* Ubick and Briggs,**
new species

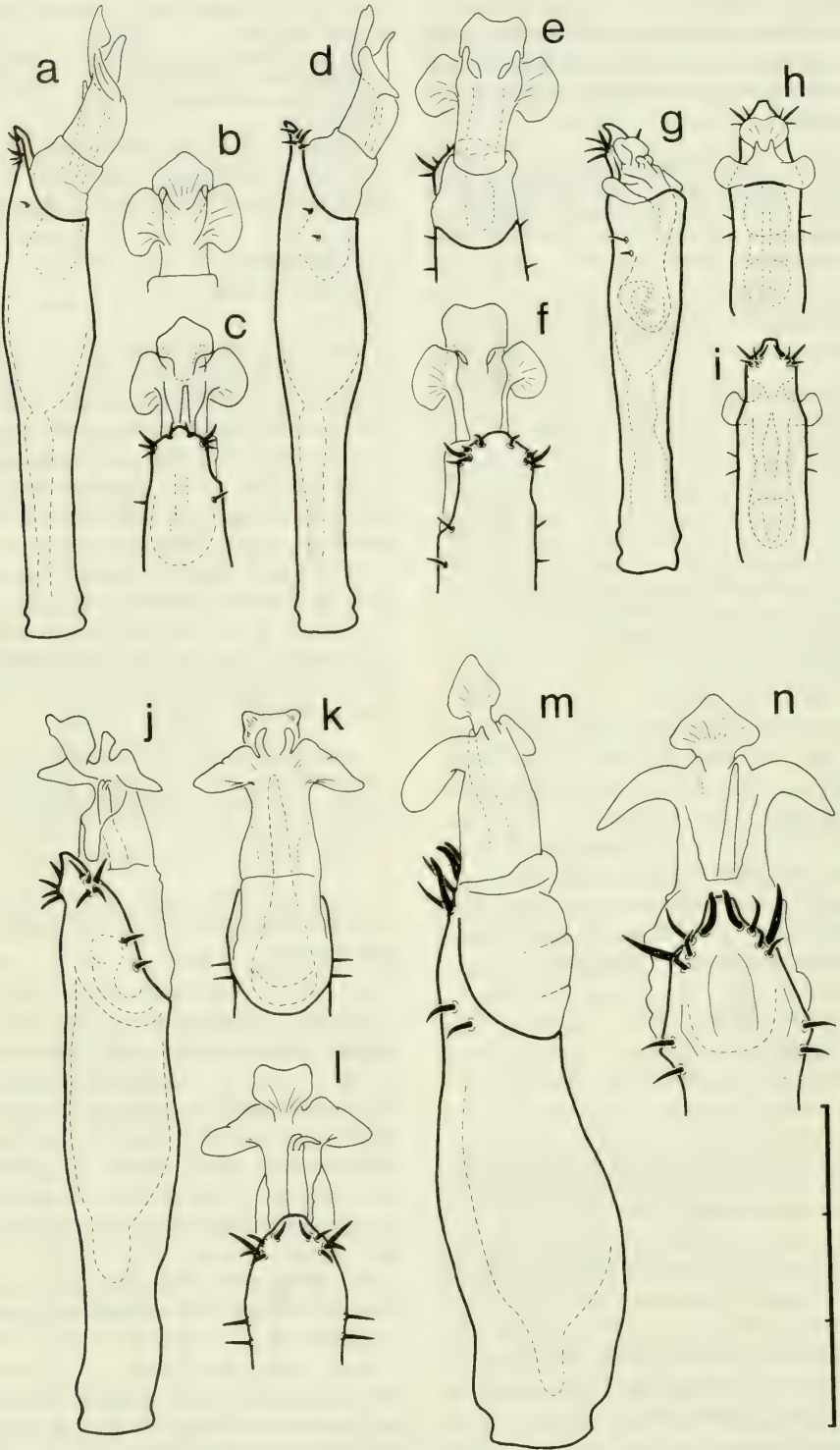
(Fig. 14m, n)

DIAGNOSIS.—Males of this species are distinguished from all others in the group in having a dorsal process with a diamond-shaped central lobe and elongated lateral lobes. Males lack the palpal spur but have an enlarged mesoapical spine-bearing tubercle on the palpal tarsus.

ETYMOLOGY.—The specific name refers to the sexually dimorphic palpal spination characteristic of this species.

DESCRIPTION.—Color yellowish orange. Carapace with 3 pairs of anterior tubercles. Eyes well developed. Tarsal count 3-4-4-5.

Male: Total body length, 1.22. Scute length, 0.86. Scute width, 0.90. Eye tubercle length, 0.17. Eye tubercle width, 0.18. Leg II length, 2.07. Palpal tarsus without dorsal spur but with enlarged mesoapical spine-bearing tubercle. Penis



with ventral plate bearing 7 pairs of setae, of which 2 distal pairs are enlarged. Dorsal process with long, tapering lateral lobes and diamond-shaped median lobe.

Female: Total body length, 1.00. Scute length, 0.63. Scute width, 0.60. Eye tubercle length, 0.13. Eye tubercle width, 0.12. Palpal tarsus without enlarged spine-bearing tubercle. Ovipositor with apical microspines, 12 apical setae, and 1 pair of subapical setae.

TYPE SPECIMENS.—Male holotype and three paratypes (two males, one female) under granite in an oak grassland at the NE entrance to Watts Valley, Fresno County, 28 Jan. 1968, TSB.

SPECIMENS EXAMINED.—Only the type series.

***Calicina mesaensis* Ubick and Briggs,**
new species

(Fig. 4b, 14j-l)

DIAGNOSIS.—Males of this paedomorphic species differ from all others in having a dorsal process with a quadrate median lobe and elongate lateral lobes.

ETYMOLOGY.—The specific name is a reference to the type locality, Table Mountain.

DESCRIPTION.—Color yellow-orange. Carapace with 2 pairs of anterior tubercles. Eyes well developed. Tarsal count 3-4-4-4.

Male: Total body length, 1.14. Scute length, 0.87. Scute width, 0.82. Eye tubercle length, 0.18. Eye tubercle width, 0.17. Leg II length, 2.02. Palpal tarsus with greatly reduced dorsal spur (Fig. 4b). Penis with 7 pairs of setae on ventral plate. Dorsal process with quadrate median lobe and tapering lateral lobes. Stylus with apical prong.

Female: Total body length, 1.13. Scute length, 0.78. Scute width, 0.71. Eye tubercle length, 0.15. Eye tubercle width, 0.13. Ovipositor with apical microspines and 7 pairs of apical setae.

TYPE SPECIMENS.—Male holotype and 25 paratypes (11 males, 14 females), under basalt rocks in an oak grassland at Table Mountain, 2.8 mi (4.5 km) N Millerton Lake Road on Sky Harbor Road, Fresno County, 31 Mar. 1985, TSB, TO, WCR, and DU. Two paratypes (male, female) deposited at the AMNH collection.

SPECIMENS EXAMINED.—Only the type series.

***Calicina breva* (Briggs, 1968),**
new combination

(Fig. 14a-c)

Sitalcina sierra breva Briggs, 1968:21.

DIAGNOSIS.—Males of this paedomorphic species may be distinguished by the structure of the dorsal process: median lobe pentagonal, subequal to the laterals, and ventral plate with only 5 pairs of setae.

ADDITIONAL DESCRIPTION.—Carapace with 1 or 2 pairs of anterior tubercles. Penis with ventral plate bearing 5 pairs of small setae; dorsal process with three subequal, cloverlike lobes; stylus short and straight. Ovipositor with apical microspines and 7 pairs of apical setae.

TYPE SPECIMENS.—Male holotype, female allotype, and five paratypes (three males, two females), under basalt rocks in a grassland at 1 mi (1.6 km) S Knight's Ferry, Stanislaus County, 11 Apr. 1967, TSB.

SPECIMENS EXAMINED.—Only the type series.

***Calicina basalta* Ubick and Briggs,**
new species

(Fig. 14d-f)

DIAGNOSIS.—This paedomorphic species is most closely related to *breva* from which it may be distinguished by the notched median lobe of the dorsal process of the penis.

ETYMOLOGY.—The specific name refers to the microhabitat of this species.

DESCRIPTION.—Color yellow. Carapace with 1 or 2 pairs of anterior tubercles. Retina occasionally absent. Tarsal count 3-4-4-4.

Male: Total body length, 1.08. Scute length, 0.70. Scute width, 0.77. Eye tubercle length, 0.13. Eye tubercle width, 0.15. Leg II length, 2.07. Palpal tarsus without dorsal spur. Penis similar to that of *breva* except that dorsal lobe has notched median lobe.

Female: Total body length, 0.86. Scute length, 0.60. Scute width, 0.63. Eye tubercle length, 0.12. Eye tubercle width, 0.12. Ovipositor with apical microspines and 7 pairs of apical setae.

FIGURE 14. Male genitalia of the *serpentinea* subgroup. 2. (a-c) *C. breva* (paratopotype), lateral, dorsal, and ventral views. (d-f) *C. basalta* (holotype), lateral, dorsal, and ventral views. (g-i) *C. macula* (holotype), sublateral, dorsal, and ventral views showing retracted glans. (j-l) *C. mesaensis* (holotype), lateral, dorsal and ventral views. (m, n) *C. dimorphica* (paratopotype), lateral and ventral views.

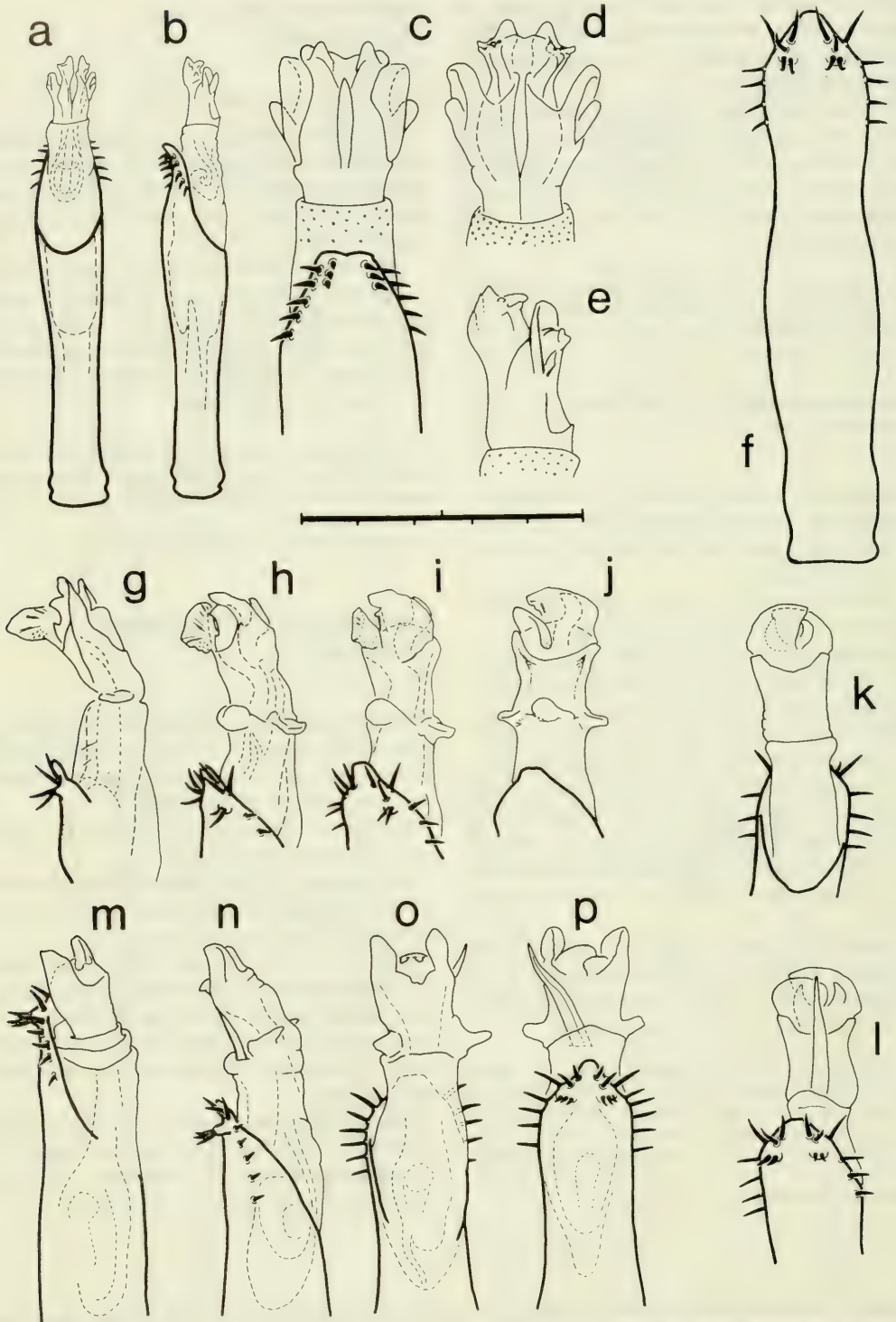


FIGURE 15. Male genitalia of the *sequoia* subgroup. (a-e) *C. diminua* (paratopotype). (a, b) Dorsal and lateral views. (c-e) Ventral, dorsal, and lateral views. (f-p) *C. sequoia*. (f) Ventral view of penis, truncus (Little River). (g-j) Lateral to ventral views (Little River). (k, l) Dorsal and ventral views (Pine Ridge Road). (m) Lateral view showing retracted glans (Mendocino). (n-p) Lateral, dorsal, and ventral views (Usal Creek). (Scale bar equals 0.25 mm, except for "c-e" where it equals 0.10 mm).

TYPE SPECIMENS.—Male holotype and five paratypes (three males, two females), under basalt rocks in a grassland area 8 mi (12.9 km) SW Jamestown, Tuolumne County, 10 Feb. 1968, TSB. Six paratypes (three males, three females) taken in similar conditions at 13 mi (21 km) E Oakdale, Stanislaus County, 10 Feb. 1968, TSB and BL.

SPECIMENS EXAMINED.—Seven males, five females.

The *sequoia* Subgroup

DIAGNOSIS.—The presence of at least 5 pairs of regularly spaced lateral setae on the ventral plate and the extremely complex dorsal process are diagnostic for this subgroup.

DISTRIBUTION.—Known from the northern Coast Ranges of California.

Calicina diminua Ubick and Briggs,
new species

(Fig. 15a–c)

DIAGNOSIS.—This pedomorphic species, the smallest *Calicina*, is most easily distinguished by the elaborate structure of the glans penis.

ETYMOLOGY.—The specific name is a reference to the small size of this species.

DESCRIPTION.—Color yellow. Carapace without anterior tubercles. Eyes, both retina and lens, absent. Tarsal count 3-4-4-4.

Male: Total body length, 0.77. Scute length, 0.49. Scute width, 0.53. Eye tubercle length, 0.08. Eye tubercle width, 0.09. Leg II length 1.41. Palpal tarsus with dorsal spur. Penis small; ventral plate with 5 pairs of lateral setae and two triads of ventral setae; dorsal process ornate; stylus short and spinelike.

Female: Total body length, 0.60. Scute length, 0.46. Scute width, 0.46. Eye tubercle length, 0.06. Eye tubercle width, 0.07. Ovipositor with only 10 apical setae and without subapical setae or microspines.

TYPE SPECIMENS.—Male holotype and 11 paratypes (four males, seven females), under serpentine on a grassland hillside at Novato, San Marin Drive, Marin County, 2 Jan. 1986, TSB and DU. Five paratypes, 0.5 km SW of type locality, 7 Dec. 1985 (male) and 28 Apr. 1968 (three males, one female), TSB. Two paratypes (male, female) deposited at the AMNH collection.

SPECIMENS EXAMINED.—Nine males, eight females.

Calicina sequoia (Briggs and Hom, 1966),
new combination

(Fig. 15f–p)

Sitalcina sequoia Briggs and Hom, 1966:267. Briggs, 1968:28.

DIAGNOSIS.—In addition to their distinctive male genitalia (dorsal process large with 1 or 2

pairs of lobes and ventral plate with 6 to 8 pairs of lateral setae) these small phalangodids have the most reduced tarsal count of any *Calicina* (3-4-4-4 or less), but unlike most other pedomorphic species, have well developed eyes.

ADDITIONAL DESCRIPTION.—Tarsal count usually 3-3-4-4, occasionally 3-4-4-4. Carapace with 1 pair of anterior tubercles. Penis with ventral plate bearing 6–8 pairs of lateral setae and 2 or 3 pairs of ventral setae; dorsal process with two pairs of lobes (the basal pair sometimes missing) and an apical portion capable of hyperextension; stylus ventral, spinelike. Ovipositor with apical microspines, 6 pairs of apical setae, 2 pairs of subapical setae, and 1 pair of apical teeth.

VARIATION.—The five specimens from the southernmost localities (Pine Ridge Road and Talmage) have the higher tarsal count of 3-4-4-4 and lack dorsobasal lobes on the dorsal process (Fig. 15k, l) but, otherwise, do not differ in genitalic features.

JUVENILES.—The only known juvenile, from Mendocino, is an early instar having a tarsal count of 1-1-2-2. As in adults, the eyes are well developed. However, the anterior tubercles are absent and the free tergites are armed with robust spines which are absent in adults.

TYPE SPECIMENS.—Female holotype, male allotype, and six paratypes, under rocks and logs in a Douglas fir forest at 2.3 mi (3.7 km) S Piercy, Mendocino County, 13 Mar. 1966, TSB and KH.

SPECIMENS EXAMINED.—Twenty-two males, 24 females, one juvenile, seven specimens of undetermined sex.

NEW RECORDS.—MENDOCINO COUNTY: 2.3 mi (3.7 km) S Piercy, 17–18 June 1966 (KH, VFL); Mendocino, 4 May 1963 (DCR); 5 mi (8 km) S Usal Creek, 17 Apr. 1976 (TSB); Pine Ridge Road, 1.6 mi (2.6 km) S Low Gap Road, W of Ukiah, 10 Feb. 1985 (TSB); Casper, 3 Aug. 1957 (JRH, GAM; AMNH collection); Talmage, 29 July 1959 (LMS, ROS; UCB collection).

NATURAL HISTORY.—This species is known from redwood and Douglas fir forests and has been collected beneath both logs and rocks. Six samples contained individuals of “*Sitalcina*” *cockerelli* Goodnight and Goodnight.

PHYLOGENY

MONOPHYLY OF *CALICINA*

Calicina is believed to be monophyletic on the basis of its unique palpal tarsus and possible synapomorphies in the ovipositor and glans morphologies. Among the Nearctic phalangodids, only the species of *Calicina* have a telescoping

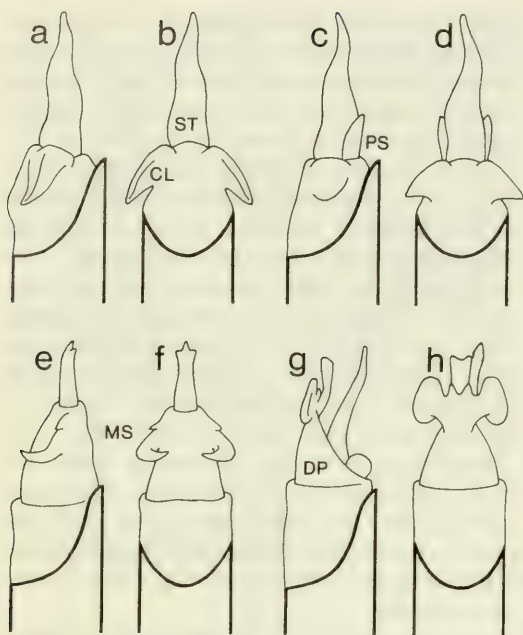


FIGURE 16. *Calicina*, glans types (a, c, e, g = lateral views; b, d, f, h = dorsal views). (a, b) *C. mariposa*, ST = stylus, CL = collar lobe. (c, d) *C. digita*, PS = parastylus. (e, f) *C. palapraeputia*, MS = middle segment. (g, h) *C. serpentina*, DP = dorsal process.

glans (Fig. 16). Representatives of all other nominal genera were examined and found to have a folding glans. At this time it is not possible to determine which of these character states is derived. Outgroup comparison cannot be used since the sister group of these (presumably closely related) genera is not known. It may be argued that the folding glans, because of its widespread occurrence, is plesiomorphic. However, the telescoping glans is functionally simpler, whereas the folding glans is usually associated with other derived genital characters, such as the bifurcate ventral plate of *Banksula* Roewer, *Texella* Goodnight and Goodnight, and all Appalachian genera.

The tarsal spur is not known in any other phalangodid genus and is, clearly, a synapomorphy for *Calicina* (Fig. 17, component 1). However, several species that we include in *Calicina* lack the spur, which we interpret to be the result of a character reversal. The tarsal spur is most strongly developed in the two least derived taxa of *Calicina* (the *mariposa* group and the *digita* subgroup) but is reduced in size or absent in most

of the remaining species. Of the 11 species that completely lack the spur, most are closely related (based on genitalic characters) to species having distinct, but small, spurs (the seven species belonging to the *kaweahensis*, *serpentina*, and *sequoia* subgroups). Likewise, on the basis of their glans structure, the two species in the *arida* subgroup and the monotypic *minor* subgroup are clearly representatives of the *digita* and *serpentina* species groups, respectively. This leaves only one unassociated species, *palapraeputia*, that lacks the spur. However, despite the unique glans structure of this species, its generic placement is not questioned because, in addition to having a telescoping glans, its ovipositor closely resembles that of some *Calicina* species in microspine distribution and setal arrangement (compare Fig. 5e, f and 5g, h).

The ovipositor of *Calicina* differs from that of *Sitalcina* in several characters (Table 1). Of these, microspines may be derived because, with few exceptions, they do not occur in other Californian phalangodid species. Also, two setal series (apical and subapical) present in most *Calicina* species have not been observed in *Sitalcina* nor in other Californian phalangodid genera. Further investigation will be necessary to determine the polarities of these character states and their universality.

SISTER GROUP

There are two possible sister groups of *Calicina*. The first consists of the genera which have a telescoping glans. Of the European phalangodids, apparently only *Ptychosoma* Soerensen has this type of glans (see figures in Brignoli 1968). Two additional species with telescoping glans have recently been described in *Scotolemon* Lucas (*espanoli* Rambla, 1973 and *balearicus* Rambla, 1977) but, based on the published genital illustrations, appear to be congeneric with *Ptychosoma*. Although similar to *Calicina* in general body structure, *Ptychosoma* differs in having a greater number of palpal spine-bearing tubercles, in having a strongly modified ventral plate, and in lacking sexually dimorphic structures.

A telescoping glans is likewise found in some Southeast Asian genera. *Buparellus* Roewer and *Bupares* Thorell have a glans structure quite similar to some *Calicina* species, but they differ in having more strongly armed palpi (see figures in Suzuki 1985). The Japanese *Parabeloniscus* Su-

TABLE 2. LIST OF CHARACTERS AND THEIR PRESUMED POLARITIES.

Character	Plesiomorphic	Apomorphic
1. male palpal tarsus	unmodified	with spur
2. parastylus	absent	present
3. stylus shape	sinuous	straight
4. parastylus insertion	ventral	(a) lateral, (b) dorsal
5. microspine distribution	distal half of ovipositor	restricted to apex
6. glans segments	two	three
7. dorsal process (DP)	absent	present
8. DP apex	bifurcate	lobate
9. basoventral lobes of DP	present	absent
10. median lobe length	shorter than paramedian lobes	longer than paramedian lobes
11. stylus length	subequal to DP	(a) longer than DP (b) shorter than DP
12. lateral lobe shape	length = width	length > width

zuki shares with *Calicina* a similar glans and ventral plate spination but has increased palpal spination and a sexually dimorphic third tergite (elongated in males) (see figures in Suzuki 1973). Although placed in the Phalangodinae, these genera also lack the characteristic eye tubercle and may belong elsewhere.

Finally, the genitalia of Assamiidae and Bian-tidae strongly resemble those of some *Calicina* species (see figures in Martens 1977, 1986). Members of these families, however, have highly modified palpi (segments are elongated and attenuated and spination is reduced) and generally lack well defined eye tubercles.

The relationship of *Calicina* to the above taxa depends on the phylogenetic significance of the telescoping glans. If this glans structure is derived, then these and additional taxa may actually be closely related. On the other hand, if the telescoping state is plesiomorphic, then differences in somatic characters assume greater importance. In this case, the somatically similar Californian phalangodids become the second group of potential candidates for the *Calicina* sister group. Of these, the most likely possibility is a recently discovered (and undescribed) phalangodid genus that has a glans that unfolds and telescopes during expansion. This relationship will be explored in a future study.

INTRAGENERIC RELATIONSHIPS

The proposed relationships among the *Calicina* species are based primarily on the male genitalia. The characters used, along with their presumed polarities, are given in Table 2 and the

resulting cladograms are presented in Figures 17 and 18.

As described earlier, four types of glans occur in *Calicina*. These appear to define the major lineages that are here recognized as species groups. Each group is defined by unique structures or character states, interpreted as autapomorphies: the *mariposa* group by dorsally grooved collar lobes, the *digita* group by parastyli, the *pala-praeputia* group by an additional glans segment, and the *serpentinea* group by a dorsal process (Fig. 16).

The *mariposa* group contains species with the simplest glans morphology (Fig. 6, 16a, b). This glans contains two segments: the basal bears a pair of collar lobes and the apical consists of a sinuous stylus. This structural simplicity is assumed to be plesiomorphic. The presence of plesiomorphic somatic characters in this group is at least consistent with this interpretation. First, *Calicina mariposa* has a tarsal count of 3-5-5-5. With the exception of a few species in the *digita* group, all other *Calicina* species have lower counts. High tarsal counts, 3-5-5-5 or higher, occur in virtually all other Holarctic phalangodids. Second, the males of all species in the *mariposa* group have well developed tarsal spurs. This state, as argued previously, is presumed to be plesiomorphic within the genus.

The glans in the *digita* group is similar to that in the *mariposa* group, but contains an additional pair of sclerites, the parastyli (PS) (Fig. 16c, d, component 2). The *digita* subgroup has ventral, scalelike parastyli and a sagittate ventral plate (Fig. 7). It is the most generalized element of the group because it retains the high tarsal count,

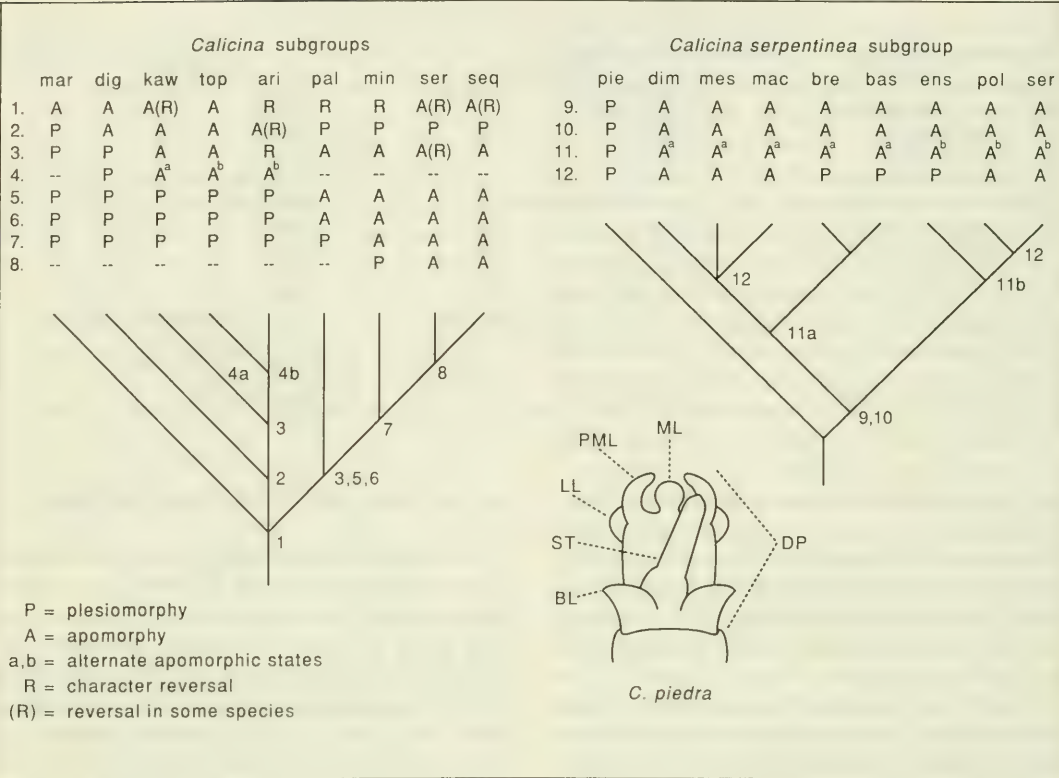


FIGURE 17. Cladogram with data matrix showing the relationships of *Calicina* subgroups using characters given in Table 2. Abbreviations: mar = *mariposa*, dig = *digita*, kaw = *kaweahensis*, top = *topanga*, ari = *arida*, pal = *palapraeutia*, min = *minor*, ser = *serpentina*, and seq = *sequoia*.

well developed tarsal spurs, and a *mariposa*-like sinuous stylus. The stylus of the *kaweahensis* and *topanga* subgroups is straight, and considered to be derived (component 3). In the former, the PS are broad, ornate, and laterally inserted (Fig. 8, component 4a). In the *topanga* subgroup the PS are rodlike and inserted dorsolaterally to the stylus (Fig. 9). The two species of the *arida* subgroup have an unusual glans morphology for their group (Fig. 10). In *arida* the PS are represented by a single dorsal rod, whereas in *cloughensis* they are totally absent. Despite the absence of PS, *cloughensis* is undoubtedly a member of this subgroup because of its close relationship with *arida*. (See the diagnosis of the subgroup for synapomorphies.) Using the *digita* subgroup as an outgroup, the dorsal position of the PS in the *arida* and *topanga* subgroups is synapomorphic (component 4b).

Calicina palapraeutia, the sole representative

FIGURE 18. Cladogram with data matrix showing the relationships of species in the *serpentina* subgroup using characters given in Table 2. The drawing is the glans, ventral view, of *C. piedra*. Abbreviations: pie = *piedra*, dim = *dimorpha*, mes = *mesaensis*, mac = *macula*, bre = *brevia*, bas = *basala*, ens = *ensata*, pol = *polina*, ser = *serpentina*, DP = dorsal process, ML = median lobe, PML = paramedian lobe, LL = lateral lobe, BL = basal lobe, and ST = stylus.

of its group, differs from all other *Calicina* species in having a three-segmented glans (Fig. 11, 16e, f). If the stylus and basal segment of this glans are homologous to comparable parts of the *mariposa* glans, the middle segment is left unassociated. One possibility is that this segment represents a highly modified PS that enveloped and fused around the stylus, as appears to occur in *kaweahensis* (Fig. 8e–g). Alternatively, the middle segment could have developed from similarly modified collar lobes from an *arida*-like ancestor (Fig. 10e–h). Either of these mechanisms would probably be accompanied by the fusion of these structures (PS or collar lobes) on the middle segment, but no evidence of this has been detected. Furthermore, both interpretations require the independent acquisition of the middle segment

lobes in *palapraeputia*. A more parsimonious alternative (and the one we accept) is that the lobes in *palapraeputia* are actually collar lobes, homologous to those found in the *mariposa* and *digita* groups. In this case the *palapraeputia* glans could be derived from a *mariposa* type through the development of an additional collar on the basal segment of the latter.

In the *serpentinea* group the glans has a derived, lobe-bearing structure, the dorsal process (Fig. 16g, h, component 7). In most species (the *serpentinea* subgroup) the dorsal process (DP) bears five apical lobes (Fig. 13, 14). The remaining three species all have unique DP morphologies. *Calicina minor*, the sole representative of its subgroup, has the simplest DP bearing a pair of dorsobasal lobes and an apical bifurcation instead of lobes (Fig. 12). Of the members of the *sequoia* subgroup, the DP of *diminua* is divided into two lateral, extremely ornate, hemispheres; whereas in *sequoia* it contains a pair of basal and apical lobes in addition to a complex apical region (Fig. 15). Despite fundamental differences in the glans structure, the last two species seem to be related as they share a unique ventral plate spination. The presence of apical lobes on the DP appears to be a synapomorphy uniting all species of the *serpentinea* group except *minor* (component 8).

The species of the *serpentinea* subgroup all have rather similar glans morphologies, with the exception of *pedra*. The *pedra* glans differs from the others in four characters: (1) DP with basal lobes, (2) paramedian lobes longer than median lobe, (3) lateral lobes wider than long, and (4) stylus subequal to DP in length (Fig. 13a–c, 18). Because basal lobes are found in the other subgroups, their presence is a synapomorphy for the entire *serpentinea* group, but a plesiomorphy at the subgroup level. The implication that *pedra* is the most generalized species in the subgroup is compatible with its relatively higher tarsal count (3-4-4-5). The remaining species in this subgroup are united in lacking basal lobes (component 9) and in having relatively larger median lobes (component 10). They are subdivided into two groups based on stylus length. Using *pedra* as the outgroup, stylus lengths either longer (component 11a) or shorter (component 11b) than the DP appear to be synapomorphic. Finally, elongated lateral lobes (component 12) are synapomorphic for some species.

Because of the *serpentinea* group's unique glans

morphology, its relationship to the other groups would appear remote. However, its ovipositor structure implies a close relationship with *palapraeputia*. In both groups the distribution of microspines is restricted to the apical surface of the ovipositor which, using *mariposa* as the outgroup, is synapomorphic (component 5). This relationship suggests that the glans morphologies in the two groups are likewise closely related; namely, that the dorsal process (DP) is homologous to the *palapraeputia* middle glans segment (component 6). The DP could conceivably have developed from the middle segment by the enlargement of the stylus opening along the ventroapical surface. In fact, the basal lobes of the DP, evident in members of all subgroups, may well be vestiges of the ventral surface of the middle segment.

Two alternative explanations for the origin of the DP are possible. First, the DP might represent highly derived parastyli. In *kaweahensis*, for example, the parastyli are greatly enlarged, partially envelop the stylus, and are fused dorsally (Fig. 8e–g). Further enlargement could result in a DP. However, this interpretation requires the concomitant loss of collar lobes in the *serpentinea* group. Second, the DP might be homologous to collar lobes. In *arida* the collar lobes are large and apically produced (Fig. 10e–h) and could conceivably form a DP through fusion and additional enlargement. However, this interpretation requires a character reversal of parastyli in the *serpentinea* group. Furthermore, both of these explanations imply a sister group relationship between the *serpentinea* group and either *kaweahensis* or *arida* which is not supported by any other known character.

BIOGEOGRAPHY

As is to be expected of cryptozoic organisms having low dispersal potential, the species of *Calicina* are allopatric or parapatric (see Fig. 19). The four known instances of sympatry, between *palapraeputia* and *ensata*, *diminua* and *polina*, *digita* and *kaweahensis*, and *digita* and *cloughensis*, are all between members of different groups or subgroups. Furthermore, these cases of sympatry may not actually involve interspecific interaction. In the last case, for example, *cloughensis* is troglobitic and *digita* epigeal. Also, though *diminua* and *polina* live in close prox-



FIGURE 19. Map of central California showing the distribution of species of *Calicina*. A black dot indicates the localities of paedomorphic species, a circle those of non-paedomorphics. Overlapping symbols denote sympatry.

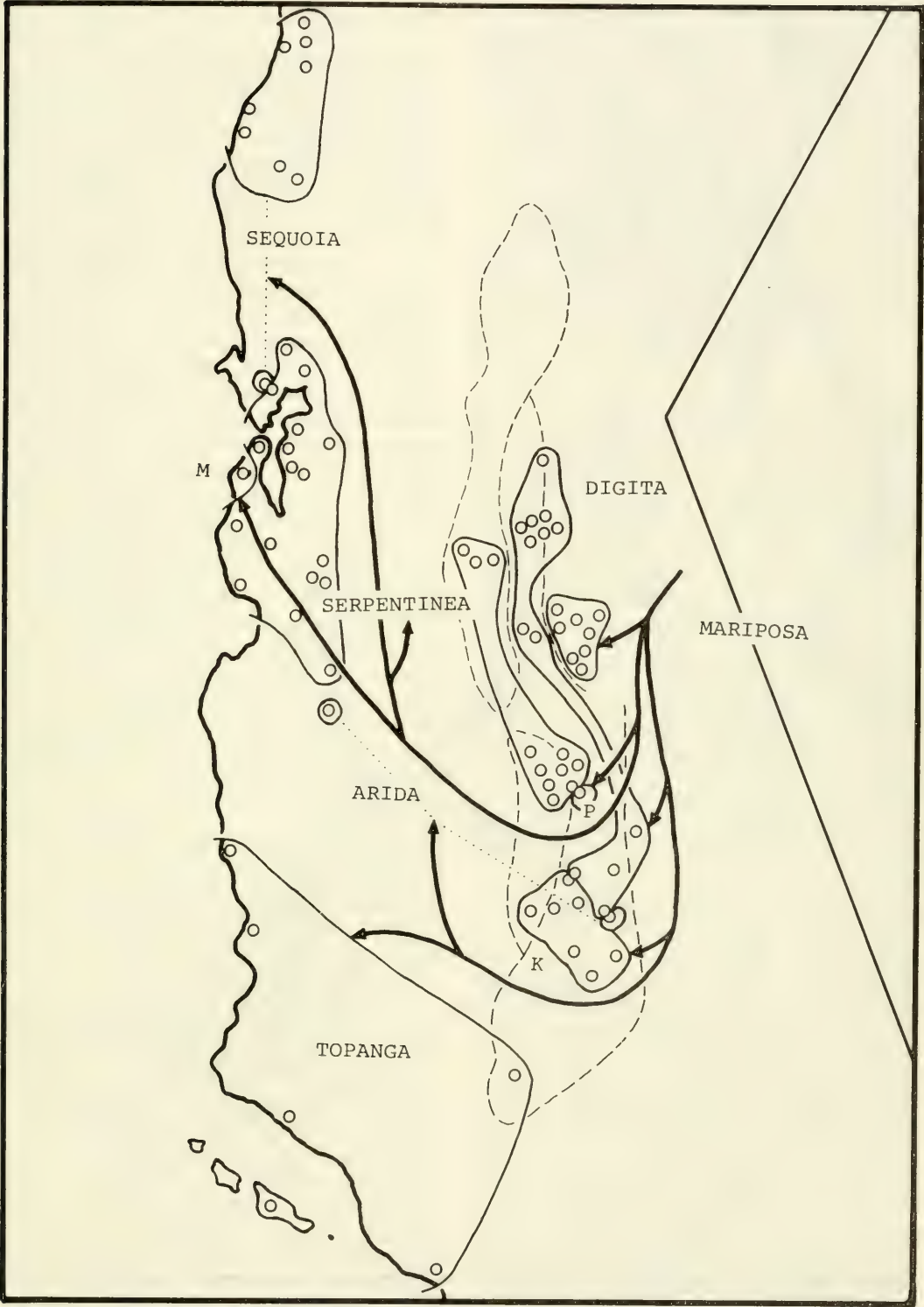


FIGURE 20. Distribution of the subgroups of *Calicina* and a cladogram of their relationships. A dotted line connects disjunct elements and a dashed line indicates the presumed boundaries of the Sierran exotic terranes (from Hendrickson 1986). Abbreviations: K = *kaweahensis*, M = *minor*, and P = *palapraeputia*.

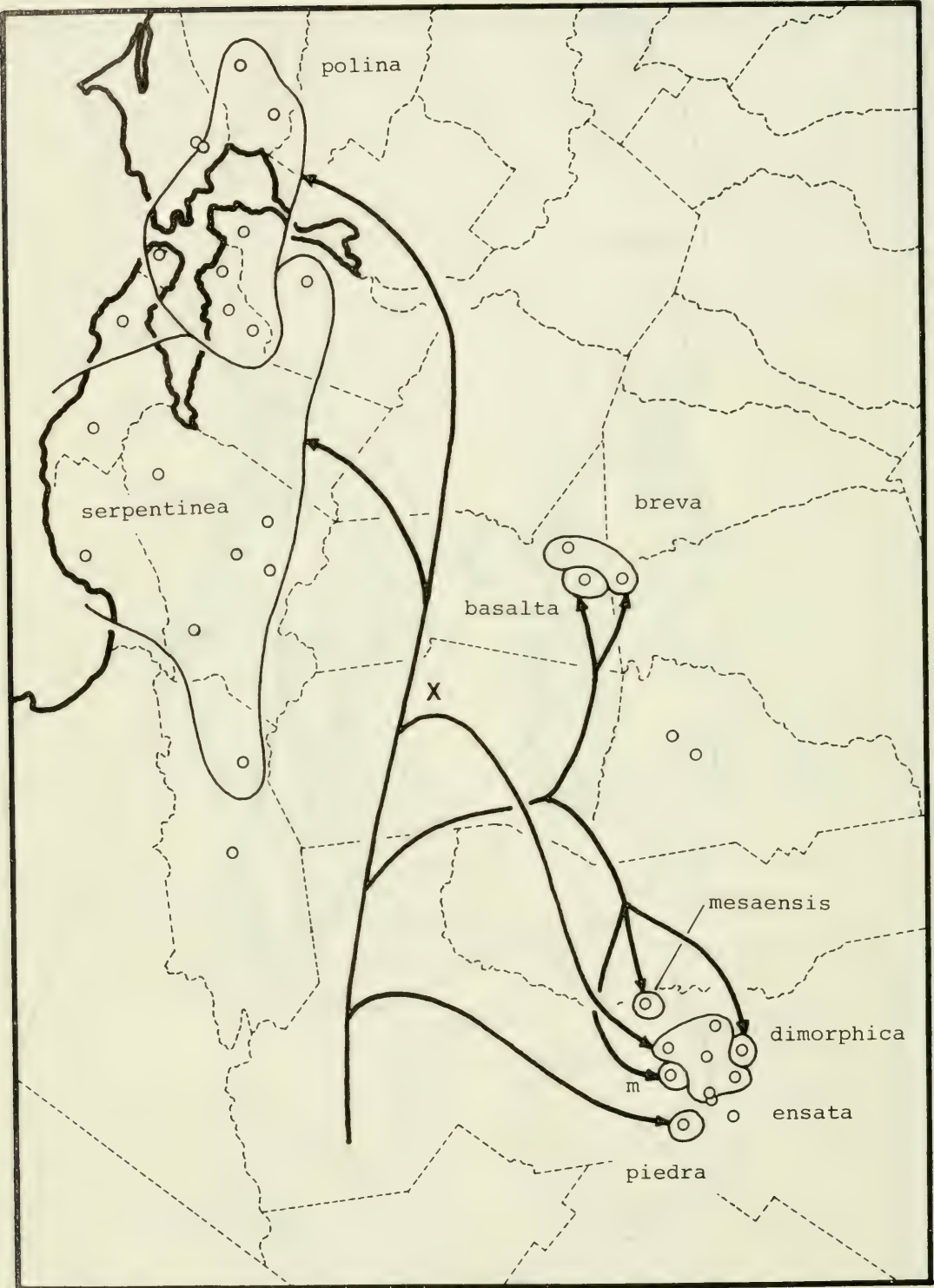


FIGURE 21. Map of central California showing the distribution of the species of the *serpentinea* subgroup with a cladogram of their relationships. The 'x' indicates the presumed time of the subgroup's disjunction by the Central Valley. Abbreviation: m = *macula*.

imity, they have never been collected in the same rock outcrops.

An area cladogram of the groups and subgroups is given in Figure 20. Two gradients are apparent. An altitudinal gradient exists between the *mariposa*, *digita*, and *serpentinea* groups, which occupy progressively lower elevations. A latitudinal gradient is also evident: the *digita* group occurs primarily along the southern mountains and coast, whereas the *serpentinea* group occupies the central and northern parts of the state.

The distribution pattern of the subgroups of *Calicina* is compatible with an origin through vicariance. The initial speciation events are likely to have taken place in the Sierra. The Sierran component of *Calicina* contains representatives of all four groups, including the most generalized members (*mariposa* group, *digita* subgroup, and *piedra*). The initial speciations may have resulted from two barriers (given the basal trichotomy) located between the ranges of the *mariposa*, *digita*, and *serpentinea* groups.

It is worth noting that these presumed barriers closely correspond to the proposed boundaries of exotic terranes given by Hendrickson (1986) and indicated in Figure 20. The coastal *Calicina* distributions also correspond closely to the maps of exotic terranes. The species *topanga* and *moroensis* each occupy separate terranes, and the coastal distribution of the *serpentinea* group (with the exception of the two westernmost *serpentinea* localities) is located within the Franciscan complex of terranes.

A few taxa exhibit disjunct distributions that, in conjunction with our knowledge of geologic history, may be used for estimating their minimum ages. The *polina* distribution surrounds the San Francisco Bay, suggesting that the species predates the formation of the bay. Similarly, *topanga* occurs on Santa Cruz Island as well as the adjacent mainland. If the currently disjunct distribution resulted from the formation of the Santa Barbara Channel, then the species must be rather old. Recent estimates for a land connection to these islands are much older (although unspecified) than the previous model of a Pleistocene land bridge (Wenner and Johnson 1980). It may be more plausible, however, that the Santa Cruz Island population represents a more recent colonization from the mainland. Rafting is a commonly evoked mechanism (for example, by Yanev (1982) for slender salamanders) and a good possibility for the forest-dwelling *topanga*.

The Central Valley is currently an obvious and impenetrable barrier for *Calicina* (owing to the absence of favorable mesic habitats) and divides the distributions of two subgroups, *arida* and *serpentinea*. The Sierran uplift, which formed the Central Valley, is thought to have begun in the early Pleistocene. A barrier could eventually have resulted from the drying effects of glacial retreats, as proposed for the populations of *Ortholasma levipes* Shear and Gruber (1983:12). Our interpretation of the *serpentinea* subgroup relationships indicates that the Central Valley could have been responsible for the disjunction of *ensata* from *serpentinea-polina* (indicated by an "x" in Fig. 21).

Another method of estimating the time of cladogenic events in *Calicina* is to use the findings for another organism from the same ancestral biota. A good example is the slender salamander, *Batrachoseps*. It appears very likely that *Batrachoseps* and *Calicina* experienced a comparable evolutionary history for three reasons: their similar habitat preferences, congruent distributions, and compatible phylogenies.

The ecological requirements of *Batrachoseps*, as described by Yanev (1980) are remarkably similar to those of *Calicina*. Both genera include species restricted to forests or oak woodlands. Both are specialized for subterranean life, appear at the surface only during favorable periods, and are able to survive in small isolates of suitable habitat. Studies on *Batrachoseps* indicate that individuals are extremely sedentary and have a very low dispersal potential, as is probably the case for *Calicina*.

The phylogeny of *Batrachoseps* consists of three main lineages. The basal branch, currently represented by two disjunct isolates, is thought to have formerly ranged along the eastern Sierra Nevada, close to that of the present distribution of the *mariposa* group. The second branch is represented by *B. attenuatus*, which has a coastal component that is almost identical to that of the *serpentinea* group and a Sierran component intersecting the distribution of *brevia* and *basalta*. The third branch contains the remaining four species whose combined distribution is very similar to that of the *digita* group.

On the basis of electrophoretic and immunological studies, Yanev (1980) proposed an origin for *Batrachoseps* in the early Eocene (ca. 50 mya). However, Hendrickson (1986) criticized these values as being far too recent and suggested that

TABLE 3. FIELD DATA OF *CALICINA*.

Taxa	N ¹	Biome	Habitat	Season ²
<i>mariposa</i> gp	10	sequoia-yellow pine	snags, logs	summer
<i>digita</i>	9	sequoia-yellow pine, oak wood, grass	logs, gra, sla	all year
<i>digita</i> (cave)	1	sequoia-yellow pine	cave	spr ³
<i>sierra</i>	6	digger pine-oak	lim, sch, sla	win-spr
<i>sierra</i> (cave)	8	digger pine-oak	caves	all year
<i>galena</i>	3	sequoia-yellow pine	gra, logs	summer
<i>kaweah</i>	12	oak wood	gra	win-spr
<i>topanga</i>	9	broadleaf evergreen, digger pine-oak, oak wood	logs, bas, snd, bre	win-spr ³
<i>kee</i>	1	oak wood	gra	win-spr
<i>mor</i>	4	grass	srp	win-spr
<i>clough</i>	3	oak wood	cave	srp-sum ³
<i>arida</i>	2	oak wood	srp	win-spr
<i>pala</i>	5	oak wood	gra, srp	win-spr
<i>minor</i>	4	grass	srp	win-spr
<i>serp</i> sbgp ⁴	29	oak wood, grass	spr, bas, gra, snd, rhy	win-spr
<i>serp</i>	12	redwood-broadleaf evergreen, digger pine-oak, oak wood, grass	logs, srp, lim, snd	all year
<i>serp</i> (cave)	1	redwood	cave	spr ³
<i>diminua</i>	3	grass	srp	win-spr
<i>sequoia</i>	11	redwood-Douglas fir	logs, rocks	all year

Abbreviations: N = number of collection samples; gp = group; sbgp = subgroup; kaweah = *kaweahensis*; kee = *keenea*; mor = *morroensis*; clough = *cloughensis*; pala = *palapraeputia*; serp = *serpentinea*; wood = woodland; grass = grassland; bas = basalt; bre = breccia; gra = granite; lim = limestone; rhy = rhyolite; sch = schist; sla = slate; snd = sandstone; srp = serpentine; spr = spring; sum = summer; win = winter.

¹ Roughly ¾ of all samples include biome and habitat data.
² Time of the year when adults are active.
³ Probably active all year.
⁴ Excluding *serpentinea*.

the isolation of *Batrachoseps* must have taken place between the late Jurassic and the early Cretaceous. This conclusion was based on the correlation between cladistic branching and geologic events, especially the history of exotic terranes. The geologic history of the Californian terranes is still largely unresolved. Most of the terranes are believed to have distant southern origins, presumably in the vicinity of southern North America. Their northward displacement as isolated units is thought to have commenced in the mid-Mesozoic. Subsequent accretions to the North American Plate range from late Jurassic to Cretaceous for the Sierran terranes, to early Eocene for the southern coastal terranes, and to late Miocene for the western elements of the Franciscan complex. If the present distribution pattern of *Calicina* is the result of isolation on terranes, then a possible scenario is that the original breakup of the Sierran terranes isolated the ancestral populations of *Calicina*, which eventually evolved into distinct species. Follow-

ing accretion to their present position, some dispersal from the terranes would be necessary to account for the present distribution, especially for the south Sierran members of the *serpentinea* group. The later arrival of the coastal terranes suggests widespread dispersal from the Sierran populations.

NATURAL HISTORY

Information on the natural history of *Calicina* comes from our field observations and the data associated with some 130 collection samples. This information, summarized in Table 3, is discussed below.

HABITAT.—Species of *Calicina* occur in mesic habitats (in conditions of total darkness and high humidity) but are apparently absent from those areas that are periodically inundated or situated in saturated soils. Most species are found exclusively beneath medium to large-sized rocks that are in contact with the soil and undisturbed. Oth-

er species also occur beneath decomposing logs. One group of species (the *mariposa* group) is found exclusively under logs and, more commonly, beneath and among fragments of fallen bark that surround large snags. Four species have been recorded from caves. One of these (*cloughensis*) is a troglobite, the others are troglaphiles with predominantly surface populations. These habitat preferences of *Calicina* are similar to those previously recorded for all Californian phalangodids (Briggs 1968) except that *Calicina*, unlike some species of *Sitalcina*, has never been collected in leaf litter.

Species of *Calicina* are associated with many rock types, the most frequent being serpentine. Of the 64 collection samples that indicate specific rock associations, 28 are from serpentine. Other frequently recorded rocks are granite (13 samples), basalt (seven), sandstone (seven), and limestone (four, excluding cave collections). The Coast Range species have been recorded primarily from serpentine and sandstone, the Sierran ones from granite and basalt.

BIOME.—The species of *Calicina* are known from a variety of biomes (see also Fig. 22). Some are apparently restricted to dense forests. Members of the *mariposa* group and *galena* are known only from high elevations (1,200–2,000 m) in primary stands of giant sequoia-yellow pine association. *Calicina sequoia* has been collected only in redwood-Douglas fir association. Three additional species have been collected in dense forests. *Calicina digita* is recorded from giant sequoia-yellow pine, *topanga* and *serpentinea* from broadleaf evergreen, the latter also in association with redwood. However, these three species are also known from more open forests (digger pine-oak and oak woodland), as well as from grassland. All remaining species are known only from oak woodland and grassland biomes.

ACTIVITY.—The period of adult surface activity varies between the species. Three patterns are evident. (1) Species active during the rainy season (winter to spring). These species (14) live in grassland and oak-woodland biomes (one species from digger pine-oak). (2) Species active during the summer. Species of the *mariposa* group and *galena*, collected in the summer months, are known only from giant sequoia-yellow pine forests. (3) Species active throughout the year. The residents of dense, low-elevation forests (*sequoia* and forest populations of *serpentinea*, *digita*, and possibly *topanga*) have a year-long adult activity

period. Likewise, the cavernicolous populations of *sierra* have been collected throughout the year. It is expected that the other cavernicolous *Calicina* also have year-round activity.

LIFE CYCLE.—Almost all individuals of *Calicina* encountered in the field and in collections are adults. Despite repeated efforts to collect juveniles, only three subadults are known from epigeal habitats (five additional juveniles are known from caves). This absence of juveniles at the surface suggests that development in *Calicina* takes place within the soil. The appearance of adults of species from drier environments coincides with the onset of the rainy season. Normally, only one or a few individuals are present on each rock or log undersurface. However, in several species we have observed aggregations of 10 or more individuals, often containing at least one mating pair.

COHABITANTS.—The habitat of *Calicina* is densely populated by a rich assortment of organisms. The most commonly observed insects are campodeid diplurans and collembolans. Observations suggest that collembolans are the likely prey of *Banksula* (Briggs and Ubick 1981) and probably also of *Calicina*.

Several laniatorid opilionids live sympatrically with *Calicina*. *Zuma* Goodnight and Goodnight is known from dense coniferous forests at higher elevations of the Sierra Nevada. *Sitalcina* is found in forests of both coastal and Sierran regions. "*Sitalcina*" *cockerelli* Goodnight and Goodnight lives in the northern coastal coniferous forests. *Banksula* is restricted to caves of the central Sierra foothills, but has never been collected sympatrically with *Calicina*.

In the central Coast Range and Sierran foothill regions, numerous spiders are repeatedly collected with *Calicina*. Some of the more common (and distinctive) are leptonetids (*Archoleptoneta*), telemids (*Usofila*), oonopids (*Orchestina* and *Scaphiella*), amaurobioids (*Blabomma*, *Calymmaria*, *Pimus*, and *Titiotus*) and many gnaphosids. Interestingly, these taxa, with the exception of the oonopids, gnaphosids, and *Pimus*, all have local cavernicolous representatives.

CONSERVATION.—Several *Calicina* species are known only from single localities and may be facing extinction as a result of habitat destruction. An extreme example is *arida* whose known range consists of several square meters in a small ravine, surrounded by extremely xeric or disturbed environments. Several additional species

TABLE 4. THE RELATIONSHIP BETWEEN PAEDOMORPHIC AND TROGLOBITIC CHARACTERS (TARSAL COUNT AND EYE LOSS) AND XERIC ENVIRONMENTS (OAK-GRASSLAND BIOMES) IN *CALICINA*.

<i>Calicina</i> species	Tarsal count	Eyesight	Biome
<i>mariposa</i> gp.			
<i>mariposa</i> sbgp.			
<i>mariposa</i>	3-5-5-5		
<i>yosemitensis</i>	3-4-4-5		
<i>conifera</i>	3-4-4-5	blind	
<i>digita</i> gp.			
<i>digita</i> sbgp.			
<i>digita</i>	3-5-5-5		xeric (most)
<i>sierra</i>	3-4-4-4		xeric
<i>kaweahensis</i> sbgp.			
<i>kaweahensis</i>	3-5-4-5		xeric
<i>galena</i>	3-5-5-5 (3-5-4-5)		
<i>topanga</i> sbgp.			
<i>topanga</i>	3-5-5-5	blind (some)	
<i>keeneae</i>	3-4-4-5		xeric
<i>morroensis</i>	3-4-4-4	blind	xeric
<i>arida</i> sbgp.			
<i>cloughensis</i>	3-5-5-5	blind	
<i>arida</i>	3-4-4-4	blind	xeric
<i>palapraeputia</i> gp.			
<i>palapraeputia</i> sbgp.			
<i>palapraeputia</i>	3-4-4-5		xeric
<i>serpentinea</i> gp.			
<i>minor</i> sbgp.			
<i>minor</i>	3-4-4-4	blind	xeric
<i>serpentinea</i> sbgp.			
<i>piedra</i>	3-4-4-5		xeric
<i>ensata</i>	3-4-4-4		xeric
<i>serpentinea</i>	3-4-4-5	blind	xeric (most)
<i>polina</i>	3-4-4-4	blind	xeric
<i>macula</i>	3-4-4-4	blind (some)	xeric
<i>mesaensis</i>	3-4-4-4		xeric
<i>dimorphica</i>	3-4-4-5		xeric
<i>breva</i>	3-4-4-4	blind	xeric
<i>basalta</i>	3-4-4-4	blind (some)	xeric
<i>sequoia</i> sbgp.			
<i>diminua</i>	3-4-4-4	blind	xeric
<i>sequoia</i>	3-3-4-4 (3-4-4-4)		

are known from single localities: *basalta*, *cloughensis*, *conifera*, *diminua*, *dimorphica*, *keeneae*, *macula*, *mesaensis*, *minor*, and *piedra*. Conservation programs will be necessary if these organisms and their habitats are to be protected.

ECOLOGY

Calicina exhibits considerable size-related interspecific variation. Larger species have relatively higher tarsal counts, darker pigmentation, greater number of anterior tubercles, larger tarsal spurs (of male palpi), and well developed eyes. These structures are reduced in size or absent in their smaller relatives. The possibility that one of these character clusters is synapomorphic is incompatible with our cladistic analysis, as neither group of species represents a clade. However, there appears to be a correlation between reduced size and xeric biomes (see Table 4 and Fig. 22). This section will explore the hypothesis that the character transformations result from two phenomena, paedomorphosis and troglobism, and represent adaptations to xeric conditions.

PAEDOMORPHOSIS.—The direction of the somatic character transformation can be inferred by comparison with the ancestral state. As argued in the phylogeny section, the probable outgroup for the remaining species of *Calicina* is *mariposa*, the species with the simplest (=plesiomorphic) glans morphology. The forest-dwelling *mariposa* is a large, strongly pigmented species, which has a high tarsal count (3-5-5-5), the greatest number of anterior tubercles (seven to eight pairs), a large tarsal spur, and well developed eyes. That the character states associated with large size are plesiomorphic is further supported by the condition in other Phalangodidae. With the exception of troglobitic species, virtually all remaining Nearctic phalangodids are large, strongly pigmented forest dwellers with high tarsal counts and well developed eyes. It is, thus, reasonable to suppose that the reduction in size and structure is derived.

Ontogenetic transformations were ascertained indirectly by examining the juvenile morphology. A total of eight specimens, representing five species, were examined (attempts to collect additional juveniles were not successful). All juveniles are white, lacking any of the orange pigmentation found in adults, all lack tarsal spurs, and all, with the exception of one penultimate instar (*galena*), lack anterior tubercles. Based on relative size, these specimens represent early (four individuals), middle (two), and penultimate instars (two). The only observable correlation with growth, other than size, is an increase in tarsal count. The earliest instars have tarsal counts of

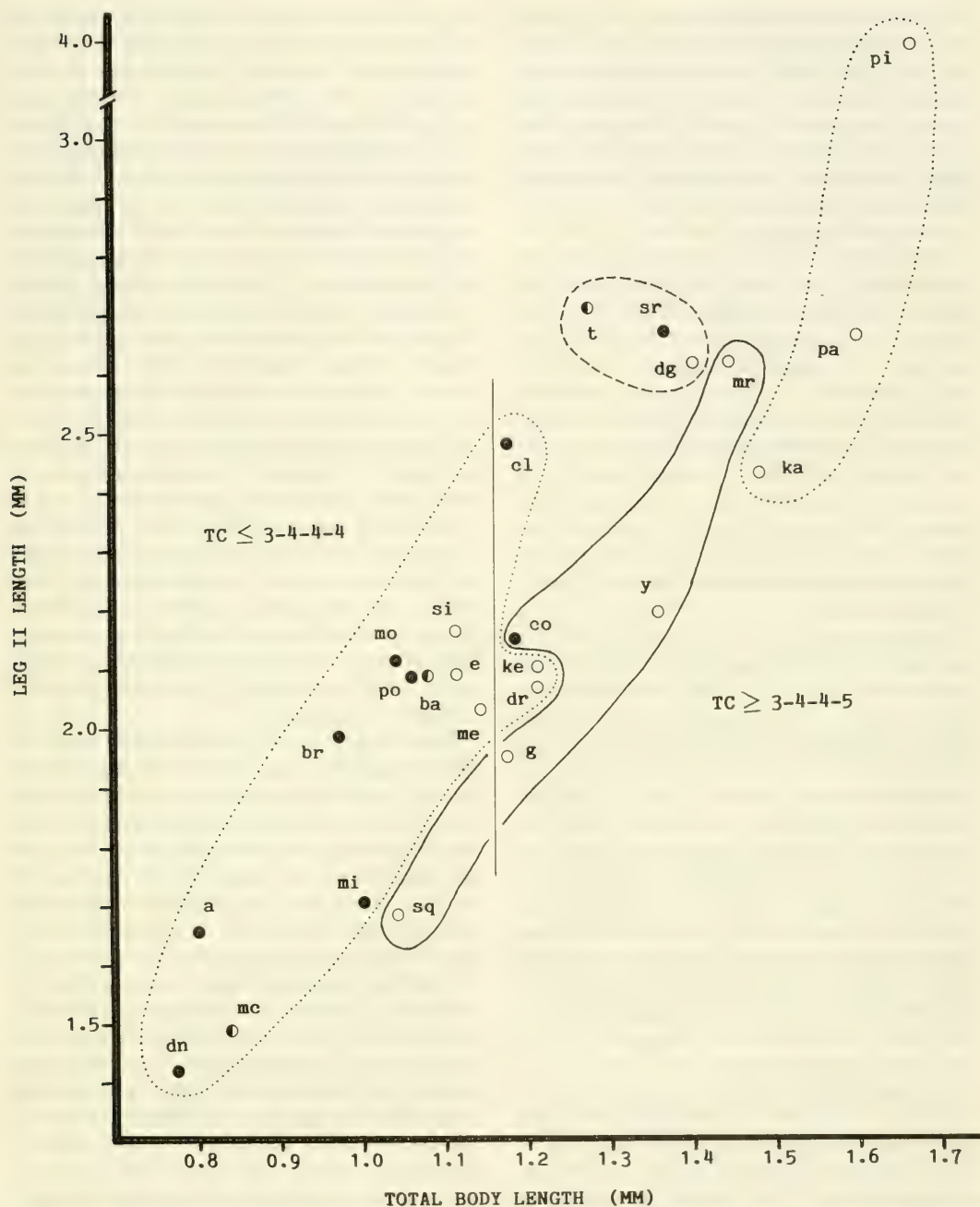


FIGURE 22. A plot showing the distribution of paedomorphic and troglotic characters in *Calicina*. The Total Body Length and Leg II Length values are from the measurements of male holotypes (male allotypes of *digita*, *kaweahensis*, *minor*, and *serpentinea*). A circle indicates species having well developed eyes, a black dot denotes blind species, and a mixed symbol indicates the species with partial retinal loss. The vertical line separates those species with tarsal counts of 3-4-4-4 or less (paedomorphics) from those with higher counts. The forest-dwelling species are encircled by a solid line, those from oak woodland and grassland by a dotted line, and those living in both densely forested and grassland biomes by a dashed line. Abbreviations: a = *arida*, ba = *basalta*, br = *brevia*, cl = *cloughensis*, co = *conifera*, dg = *digita*, dn = *diminua*, dr = *dimorphica*, e = *ensata*, g = *galena*, ka = *kaweahensis*, ke = *keenea*, mc = *macula*, me = *mesaensis*, mi = *minor*, mo = *morroensis*, mr = *mariposa*, pa = *palapraeputia*, pi = *piedra*, po = *polina*, si = *sierra*, sq = *sequoia*, sr = *serpentinea*, t = *topanga*, and y = *yosemitensis*.

1-1-2-2 (*sierra* and *sequoia*) and 1-2-2-2 (*cloughensis*); later instars (*serpentinea*) have 2-2-3-3; and the oldest (*galena*), 3-5-4-5. Eyes are present in species with eyed adults (*sierra*, *galena*, and *sequoia*), absent in the others (*cloughensis* and *serpentinea*). Despite the small sample size, it seems probable that these observations apply to all *Calicina*, given the generally conservative nature of juvenile characters.

Using *mariposa* as the outgroup, the character states found in the small species of *Calicina* are derived. However, a comparison with their presumed ontogeny indicates that they are plesiomorphic. The inescapable conclusion is that the small species are derived through the retention of juvenile characters; namely, that they are paedomorphic. The other possible alternative is that the juvenile states are in reality character reversals; i.e., that penultimate instars have adult somatic morphology. However, this latter possibility is clearly less parsimonious and not supported by the morphology of the two penultimate instars examined.

Paedomorphosis is a widespread phenomenon in *Calicina*. With the exception of three species (*mariposa*, *digita*, and *topanga*), all species have some degree of paedomorphic modification. However, only the 12 species having the lowest tarsal counts (3-4-4-4; 3-3-4-4 in *sequoia*) and the high correlation to other characters (see Fig. 22) are here considered to be significantly paedomorphic. Given our phylogenetic interpretations, paedomorphic species are present in all subgroups except *mariposa*, *kaweahensis*, and *palapraeputia*, and must have evolved independently at least nine times. Most of the paedomorphics (nine) belong to the *serpentinea* group; the remainder belong to the *digita* group, where they occupy the periphery of the group's distribution (see Fig. 19).

Paedomorphosis has been well documented in Opiliones. In her review, Rambla (1980) listed many examples of the phenomenon in Caddidae, Ischyropsalidae, Nemastomatidae, and Pentanychidae. Briggs (1986), in addition to pointing out the presence of paedomorphic *Calicina* (as *Sitalcina*) species, included Triaenonychidae among the examples.

TROGLOBISM.—Although only one species of *Calicina* (*cloughensis*) is an obligate cavernicole, troglotic characters are found in many species of *Calicina*, including most paedomorphics. The most obvious character is eye loss. Eight of the paedomorphic species lack retinæ, along with

three non-paedomorphics (excluding *cloughensis*). However, eye loss does not appear to be a paedomorphic character, as juveniles of eyed species have well developed eyes (for example, the early instars of *sierra* and *sequoia*). Additional character states of paedomorphics, such as pale coloration and small body size, could also be troglotic adaptations. Another common troglotic character is increased appendage length. Preliminary results (Fig. 22) suggest that the blind species of *Calicina* have slightly longer leg II lengths than comparable-sized eyed ones.

SELECTIVE PRESSURES.—In his exhaustive study of heterochrony, Gould (1977) differentiates two distinct phenomena included in paedomorphosis: progenesis and neoteny. Progenesis evolves (through r selection) in harsh, unstable, density-independent situations that favor rapid maturation. This is achieved by shortening the life cycle through premature maturation, and results in adults juvenilized in both size and shape. Neoteny, on the other hand, evolves (through K selection) in stable, density-dependent situations that favor maintenance. Here the selection is not for early maturation but for adaptive larval characters. Adult neotenis are, therefore, juvenilized in shape but not size.

The small size of paedomorphic *Calicina* strongly suggests progenesis. As mentioned earlier, all paedomorphic species (except *sequoia*) reside exclusively in oak woodland and grassland biomes, whereas non-paedomorphics occur predominantly in dense forests. The former biomes are much more xeric and experience severe dry seasons, which may favor both the small size and shorter life cycle of progenetics. The presence of troglotic characters in paedomorphic *Calicina* indicates a prolonged subterranean existence, which would clearly favor a reduction in size. Also, a shorter life cycle would be an advantage in harsh environments having short growing seasons. This was postulated by Shear (1975) for another progenetic harvestman, *Caddo pepperella* Shear.

A somewhat weaker argument may be made that the paedomorphosis in *Calicina* is the result of neoteny. First, it is theoretically possible (though perhaps less parsimonious) that the reduction in size and juvenilization are independently derived; the former resulting from proportioned dwarfism, the latter from neoteny. Second, the presence of troglotic characters in paedomorphic *Calicina* suggests cavelike selective pressures. Studies cited by Culver (1982)

indicated that certain cave salamanders become neotenic in response to a low food supply. If the subterranean habitat of paedomorphic *Calicina* is cavelike in these respects, such as constant conditions and resource scarcity, then K. selection and neoteny emerge as possibilities.

Neoteny is also a possibility for the three largest species of *Calicina*: *kaweahensis*, *palapraeputia*, and *piedra*. In contrast to the forest-dwelling habits of other large species, these species inhabit grassland biomes. They exhibit some reduction in the tarsal count, most pronounced in the latter two (which also lack tarsal spurs on the male palpi). Large size in combination with juvenile structures suggests neoteny.

Two situations suggest a relationship between competition and paedomorphosis. First, *Calicina sequoia* is unique among the paedomorphic species. On the basis of its low tarsal count (most populations have 3-3-4-4), it is the most paedomorphic species. However, it has well developed eyes, lives in dense forests, and has a year-round activity period. Paedomorphosis here does not seem to be a response to xeric environment. Interestingly, this species is fully sympatric with another phalangodid, "*Sitalcina*" *cockerelli*. The two species not only occupy the same biomes, but share identical habitats (we have six samples containing both species). They differ most strikingly in size: *cockerelli* has a body length two to three times that of *sequoia*. It seems conceivable that paedomorphosis could have evolved in *sequoia* as a means of reducing competition for similar prey.

Second, competition may also be involved in the evolution of paedomorphosis in other *Calicina* species. The Coast Range species, from *polina* south to *morroensis*, are closely sympatric with species of *Sitalcina*. However, *Sitalcina* species are non-paedomorphic forest dwellers, whereas the coastal *Calicina* species are predominantly paedomorphics from oak woodland and grassland biomes (except for some populations of *serpentinea*). Since the original biomes for *Calicina* were most probably dense forests, it is likely that the coastal *Calicina* species also resided in forests. Perhaps *Calicina* was excluded from the more favorable environments by *Sitalcina*.

ACKNOWLEDGMENTS

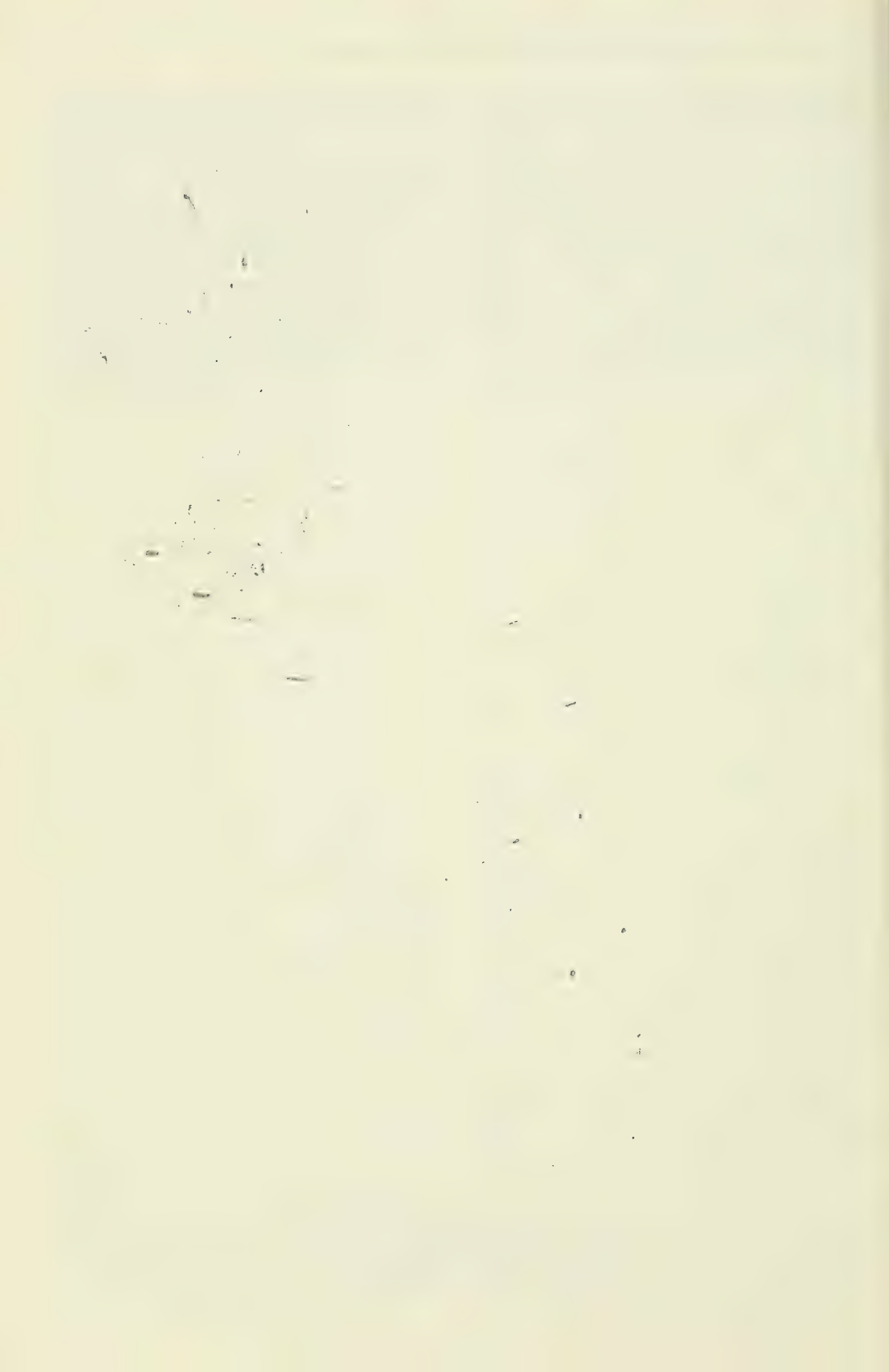
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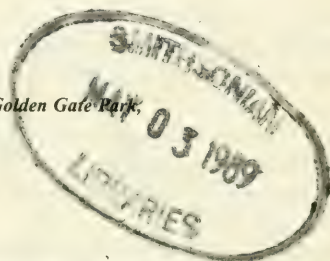
Vol. 46, No. 5, pp. 137-150, 6 figs.

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FIVE NEW BERRY-FRUITED SPECIES OF TROPICAL AMERICAN MELASTOMATACEAE

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ABSTRACT: Five species of berry-fruited Melastomataceae are described as new: *Blakea fuchsoides* from western Panama; *Clidemia hammelii* from Costa Rica, Panama, and western Colombia; *Miconia calocoma* and *M. dissitiflora* from Costa Rica; and *Tococa croatii* from eastern Panama. Predaceous mites of the genus *Ololaelaps* are recorded as residents in the foliar pocket domatia of *C. hammelii*. This is the first report of an association between a mite and a species of Melastomataceae. Discussions, distributional notes, and diagnostic illustrations are provided for each of the species.

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INTRODUCTION

Ongoing field work in little-explored areas of Central America and the study of numerous collections sent for identification continue to yield many new taxa among the berry-fruited genera of Melastomataceae. In this paper I describe new species in *Blakea*, *Clidemia*, *Miconia*, and *Tococa*. The taxonomic notes and discussions included here emphasize the diagnostic characters that make each of the new species unusual or anomalous additions to their respective genera.

Blakea fuchsoides Almeda, sp. nov.

Figure 1

TYPE:—PANAMA. Chiriquí: La Fortuna area, ca. 7 mi N of Los Planes de Hornito in forest along small draw, elev. 3,600 ft (1,097 m), 26 Aug. 1983, *Hammel & Kress* 13473 (holotype: CAS!; isotype: DUKE).

Frutex epiphyticus. Ramuli sicut petioli folia subtus inflorescentia hypanthiaque modice pilis castaneis laevibus (0.5–) 1–1.5(–2.5) mm longis armati. Petioli 0.8–2.4 cm longi, lamina 3–8.9 × 2–4.7 cm elliptico-ovata vel ovata apice acuminata basi rotundata vel subcordata, 5-nervata, membranacea vel

subcoriacea et integra vel obscure dentata. Flores 6-meri in quoque nodo superiore singuli vel bini, pedicellis 3.2–11.5 cm longis, bractaeae elliptico-lanceolatae; bractaeae exteriores 3–4.5 × 1 cm acutae liberae; bractaeae interiores 2.2–3.5 × 0.9–1.2 cm acutae liberae. Hypanthium (ad torum) 5–7 mm longum extus strigillosum; calycis tubus 5 mm longus, lobis 4–6 mm longis. Petala 19–23 × 14–15 mm elliptico-ovata apice rotundato. Filamenta 5–7 mm longa; antherae 2–3.5 × 2 mm oblongae lateraliter non cohaerentes apicaliter biporosae; connectivum dorsaliter ca. 0.5 mm supra thecarum basim inconspicue tuberculatum. Stylus 1.8–3.2 cm; ovarium 6-loculare omnino inferum apice glabro (cono et collo non evoluta).

Pendent viny epiphytes or hemiepiphytes adhering to the bark of host trees by adventitious roots. Older cauline internodes glabrate, terete, becoming striate or cracked in age. Distal indument of smooth rusty brown hairs (0.5–) 1–1.5(–2.5) mm long. Leaves of a pair slightly unequal in size; petioles 0.8–2.4 cm long; blades membranaceous to subcoriaceous, 3–8.9 cm long and 2–4.7 cm wide, elliptic-ovate to ovate, acuminate at apex, broadly rounded to subcordate at base, margin typically entire but varying to

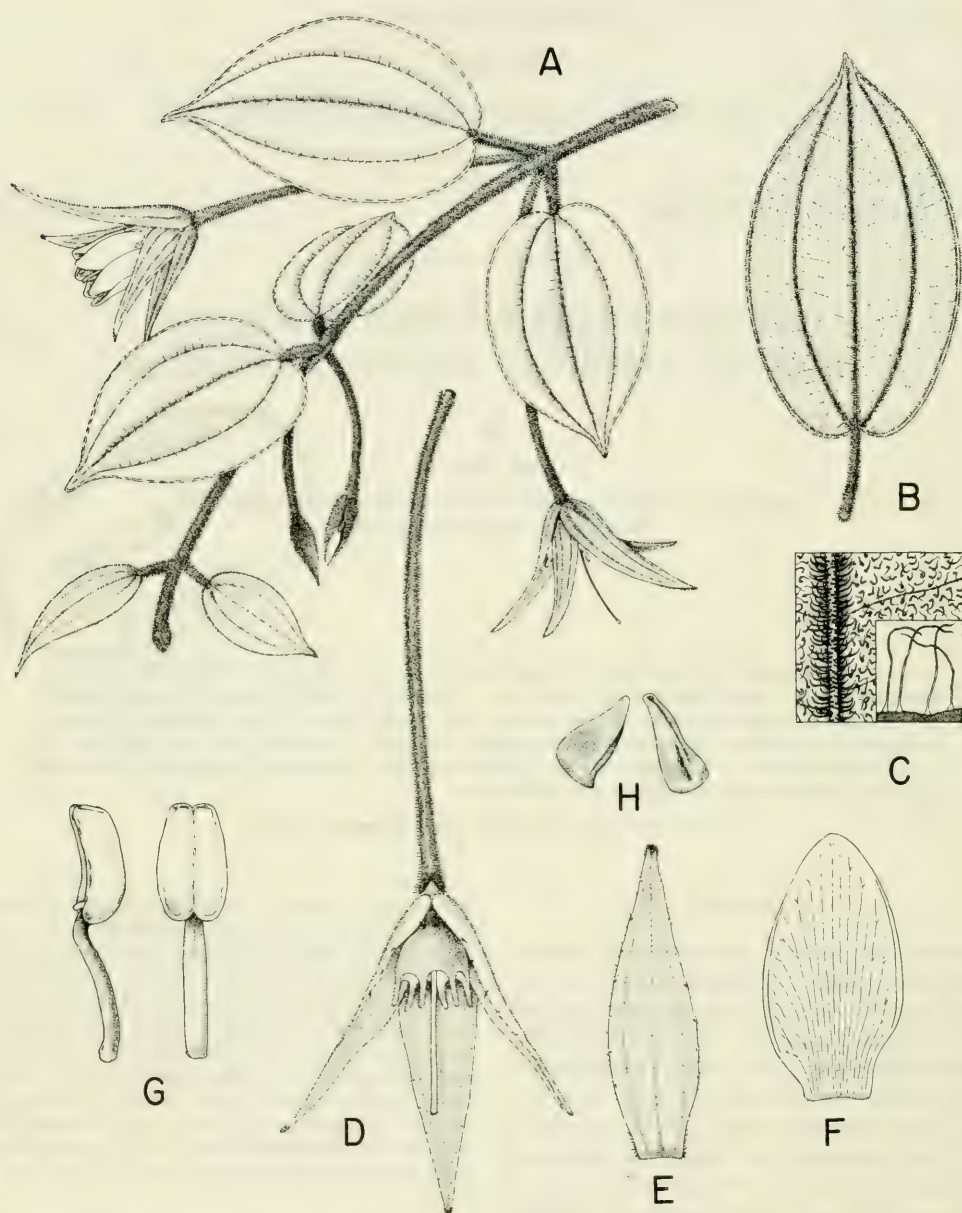


FIGURE 1. *Blakea fuchsioides* Almeda. A, habit, $\times$ ca. $\frac{2}{3}$; B, representative leaf (lower surface), $\times$ ca. $\frac{2}{3}$; C, enlargement of lower leaf surface showing pubescence and elevated median nerve; D, representative flower with petals and stamens removed, $\times$ $\frac{3}{4}$; E, outer floral bract (adaxial surface), $\times$ 2; F, petal, $\times$ 4; G, stamens, lateral view (left) and ventral view (right), $\times$ ca. 15; H, seeds, $\times$ ca. 15. (A–F from the holotype; G from Hammel 2261.)

remotely dentate, 5-nerved below, the outermost pair of subparallel primaries often inconspicuous and concealed by the revolute margins on drying, the transverse secondaries essentially parallel on the upper surface and diverging from the ele-

vated primaries at nearly right angles, moderately to densely strigillose to velutinous above with widely to antrorsely spreading smooth hairs, (0.5–)1–1.5 mm long, but often varying to glabrate at maturity with the pubescence persisting

to varying degrees in the furrows created by the impressed primary nerves, moderately to densely hirsute below with smooth rusty brown hairs 1–2.5 mm long. Flowers 6-merous, pendent, solitary, or rarely geminate in the axils of distal branches; pedicels 3.2–11.5 cm long, densely covered with minutely roughened brown spreading hairs 1 mm long. Floral bracts red, foliaceous, sessile, and entire, moderately to densely covered with roughened spreading hairs 0.5–1 mm long on both surfaces; outer bracts 3–5-nerved, free to the base, $3\text{--}4.5 \times 1$ cm, lanceolate, apex acute, base truncate to rounded; inner bracts 7–14-nerved, free to the base, $2.2\text{--}3.5 \times 0.9\text{--}1.2$ cm, lanceolate, apex acute, base truncate to rounded. Hypanthia (at anthesis) campanulate, 5–7 mm long to the torus (vascular ring), moderately to densely strigillose with obscurely roughened hairs 0.5 mm long. Calyx tube ca. 5 mm long, flaring and flangelike; calyx lobes copiously pubescent with minutely roughened brown hairs 0.25–0.5 mm long, deltoid basally between sinuses but abruptly tapered into linear-oblong, mostly entire segments 4–6 mm long and 1 mm wide. Petals glabrous, pink (fide *McPherson 7733*) or magenta (fide *Hammel & Kress 13473*), elliptic-ovate, 19–23 mm long, 14–15 mm wide, connivent and somewhat concave adaxially with slightly involute margins when expanded, apex rounded. Stamens 12, isomorphic, free and forming a pendent circle around the style; filaments complanate, 5–7 mm long; anthers linear-oblong to ovoid-oblong, truncate at apex, 2–3.5 mm long, 2 mm wide, each anther tipped with two confluent pores; connective slightly thickened dorsally and dilated basally about 0.5 mm above base of anther thecae into a bluntly rounded deflexed caudiform appendage about 0.5 mm long. Ovary inferior, 6-celled, glabrous at apex but not expanded into a cone or collar. Style straight, glabrous, 1.8–3.2 cm long, typically exerted beyond the petals and sometimes exceeding the subtending pair of floral bracts; stigma truncate to slightly rounded. Berry globose, about 1 cm long and 1 cm in diameter. Seeds numerous, clavate to narrowly pyriform or bluntly deltoid, 1(–1.5) mm long, beige with a smooth glossy testa and a prominent lateral raphe.

ADDITIONAL SPECIMENS EXAMINED.—PANAMA. Bocas del Toro: along trail on divide separating Chiriquí and Bocas del Toro, ca. $08^{\circ}45'N$, $82^{\circ}15'W$, 22 Oct. 1985, *McPherson 7199* (CAS); Fortuna Dam region along continental divide trail,

$08^{\circ}45'04"N$, $82^{\circ}15'W$, 23 Dec. 1986, *McPherson & Aranda 10062* (CAS). Bocas del Toro/Chiriquí Border: above Fortuna Dam, ca. $08^{\circ}45'N$, $82^{\circ}15'W$, 3 Dec. 1985, *McPherson 7733* (CAS). Chiriquí: road to Fortuna Dam site N of Gualaca, 22.7 mi [36.8 km] beyond bridge over Rio Esti, 22 Nov. 1979, *Antonio 2770* (CAS); La Fortuna hydroelectric project, on ridge behind camp, 22 Mar. 1978, *Hammel 2261* (MO); trail west from Fortuna Dam camp to La Fortuna, $08^{\circ}43'N$, $82^{\circ}14'W$, 23 Mar. 1985, *Hampshire & Whitefoord 903* (BM); 2 km S of Fortuna Lake, trail east, $08^{\circ}43'N$, $82^{\circ}14'W$, 24 Mar. 1985, *Hampshire & Whitefoord 912* (BM); campamento Bijao en Fortuna, 20 Mar. 1976, *Mendoza et al. 249* (PMA, US); entre alto de Guayabo y la línea divisoria continental, 25 Sep. 1976, *Correa et al. 2837* (PMA, US).

DISTRIBUTION.—Known only from the wet cloud forests of the Fortuna Dam region in western Panama along the Chiriquí/Bocas del Toro border at 1,097–1,400 m.

PHENOLOGY.—Flowering specimens have been collected from August through December; the only available fruiting collection was made in March.

Labels on collections of this species describe it as a climbing or pendent epiphyte. I have not studied this species in the field but its climbing habit, adventitious roots, and pendent inflorescences lead me to suspect that it will ultimately be shown to be a secondary hemiepiphyte like *Miconia arboricola* Almeda (Almeda 1984). Secondary hemiepiphytes are vine-like plants that germinate terrestrially, ascend nearby trees by adventitious roots, and later become epiphytic by losing root contact with the ground (Putz and Holbrook 1986).

In addition to its copious cover of brown smooth hairs on distal branchlets, petioles, lower leaf surfaces, and floral bracts, *B. fuchsoides* is distinguished by an extraordinary combination of floral characters. As emphasized by the specific epithet, the flowers of this species are reminiscent of *Fuchsia* (Onagraceae) in posture and coloration. In *B. fuchsoides* the flowers are borne on flexible pendent pedicels exposing floral organs in a way that favors hovering pollinators. The connivent petals form a broad tube-like conformation, and the floral parts are vividly colored. The hypanthia, calyx lobes, and decussate floral bracts that closely subtend the flowers are bright red, whereas the petals are reportedly pink or magenta.

If future field observations confirm that flowers of this species produce nectar, we can predict that this species is probably bird pollinated be-

cause it exhibits so many of the features associated with ornithophily (Percival 1965; Faegri and van der Pijl 1971; Proctor and Yeo 1973).

This species and other undescribed Central American species currently under study (Almeida, in prep.) exhibit anther characters that weaken the tenuous distinction between *Blakea* and the closely related segregate genus *Topobea*. The traditional differences between these genera are based on anther shape and the relative size and proximity of the apical pores. In *Blakea*, the anthers are oval, oblong, or elliptic and blunt or broadly rounded at the summit with two typically well-separated (often minute) apical pores. In *Topobea*, the anthers are linear-oblong to lanceolate or subulate with the dorsally inclined apical pores approximate and often confluent. Anther size and shape in *B. fuchsioides* agree with the syndrome typically found in *Blakea*. The broad confluent pores, however, dictate assignment of this species to *Topobea*. The truncate position of the anther pores is characteristic of neither genus and underscores the difficulty of assigning unusual new species to either of the genera as they are currently defined. Until a counterargument can be advanced for the continual recognition of *Topobea* based on something other than arbitrary characters, it seems appropriate to follow Baillon (1879) and Macbride (1941) in submerging *Topobea* in the older and much larger genus, *Blakea*.

Because *B. fuchsioides* is one of the most unusual species yet to be described in *Blakea*, it is not surprising that its relationships are obscure. A peculiar feature which has not been reported in other species of *Blakea* or *Topobea* is the delicate, veil-like membrane that covers the broad anther pores prior to anthesis. These veil-like coverings may well function to preclude excessive intrafloral pollen dispersion prior to petal expansion on the pendent flowers.

***Clidemia hammelii* Almeida, sp. nov.**

Figure 2

TYPE.—COSTA RICA. Heredia: Finca La Selva, OTS [Organization for Tropical Studies] Field Station on Río Puerto Viejo just E of its junction with Río Sarapiquí, elev. about 100 m. Slopes along Q. El Salto, 2,900 m S, 2 Sep. 1980, *Hammel 9682* (holotype: CAS!; isotype: DUKE).

Frutex vel arbuscula 1–5 m. Ramuli teretes primum sicut folia novella inflorescentia sparse vel modice setosi pilis 2–3.5 mm longis et modice vel sparse stellulato-furfuracei demum glabrati. Petioli 1–4 cm longi; lamina 11.5–29 × 6.1–14.5 cm

elliptica apice acuminata basi acuta vel cuneata, 5–7-nervata vel 5–7-plinervata, nervi in axillis acarodermatidis instructi. Inflorescentia primum terminalis demum lateralis pauciramosa plus minusve deflexa; flores 5-meri, pedicellis (ad anthesim) 1–2.5 mm longis, bracteolis 1.5–2.5 mm longis subulatis persistentibus. Hypanthium (ad torum) 1.5–2.5 mm longum; calyx primum in cono apiculato clausus demum in lobos irregulares persistentes ruptus, dentibus exterioribus 0.5–1 mm eminentibus. Petala 3–3.5 × 1–1.5 mm oblonga-rotundata glabra. Stamina isomorphica vel paulo anisomorphica glabra; filamenta 1.5–2 mm longa; antherarum thecae 1–1.25 × 0.5 vel 1.25–1.75 × 0.5 mm oblongae, poro paulo dorsaliter inclinato; connectivum nec prolongatum nec appendiculatum. Stylus 5–6 mm glaber in ovari collo 0.5 mm immersus; ovarium 5-loculare omnino inferum apice modice glanduloso-setuloso.

Shrubs or small trees 1–5 m tall. Internodes terete, glabrate at maturity; distal branchlets, vegetative buds, and inflorescences beset with a sparse to moderate covering of smooth, spreading hairs (2–3.5 mm) that is typically intermixed with inconspicuous, early deciduous, asperous-headed hairs and underlain by a moderate to dense understory of stellulate-furfuraceous or short asperous-headed hairs. Leaves of a pair typically somewhat unequal in size; petioles 1–4 cm long; blades membranaceous, 11.5–29 cm long and 6.1–14.5 cm wide, elliptic, apex long-acuminate, base acute to cuneate, margin entire to inconspicuously crenulate, 5–7-nerved or 5–7-plinerved abaxially with pocket domatia typically formed in the angle between the median nerve and each of the two proximal lateral nerves, moderately strigose to subhirsute above with smooth hairs mostly 1–2 mm long, moderately hirsute below with a mixture of smooth hairs (1–2.5 mm long) and minute glandular hairs essentially restricted to the elevated primary and higher order venation. Inflorescence a pseudolateral modified dichasium, 3–6 cm long, divaricately branched from the base; bracts of the rachis nodes paired, narrowly lanceolate to subulate, 3–3.5 mm long, 1 mm wide, sparingly stellulate-furfuraceous to glabrate; bracteoles sessile, persistent, paired but sometimes fused into an inconspicuous nodal collar, narrowly lanceolate to subulate, 1.5–2.5 mm long, up to 0.5 mm wide, essentially glabrous and entire but terminating in a solitary hair. Pedicels 1–2.5 mm long, sparingly to moderately stellulate-furfuraceous and basally encircled by a deciduous, tufted ring of barbellate or asperous-headed hairs. Hypanthia (at anthesis) campanulate, 1.5–2.5 mm long to the torus (vascular ring), moderately to sparsely covered with spreading smooth hairs 0.5–2 mm

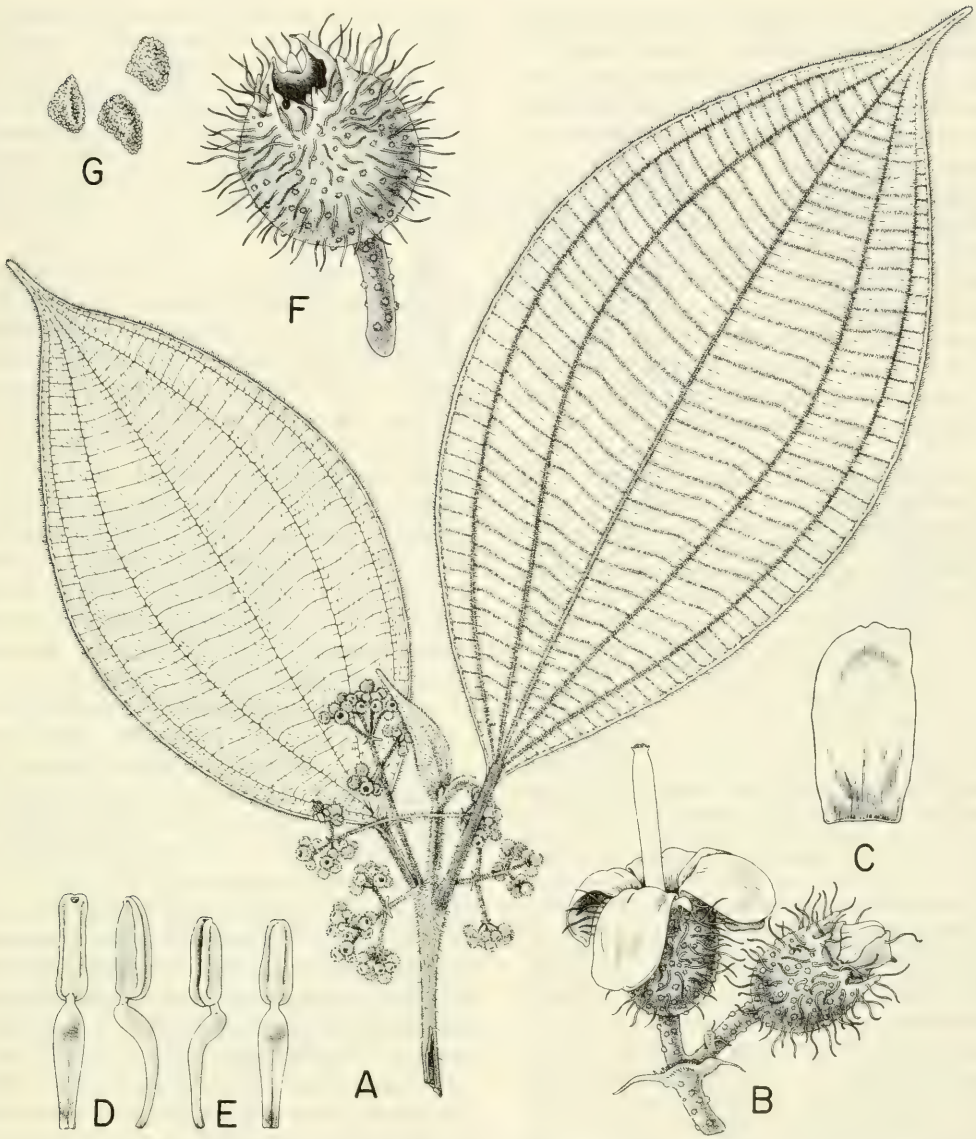


FIGURE 2. *Clidemia hammelii* Almeda. A, habit, $\times \frac{3}{4}$; B, representative flower with stamens removed (left) and floral bud showing rupturing calyx (right), $\times 9$; C, petal, $\times 10$; D, larger (antepetalous) stamens, dorsal view (left) and $\frac{3}{4}$ lateral view (right), $\times$ ca. 10; E, smaller (antesepalous) stamens, $\frac{3}{4}$ lateral view (left) and dorsal view (right), $\times$ ca. 12; F, mature berry, $\times 3$; G, seeds, $\times 16$. (A from Folsom 5864; B-E from de Nevers 3962; F, G from Hammel 12668.)

long and a sparse understory of sessile stellate-furfuraceous hairs. Calyx closed in bud and crowned by an apiculum 0.5 mm long but rupturing irregularly at anthesis into 3–5 hyaline, persistent, rounded lobes 0.5 mm long; calyx teeth 5, subulate, 0.5–1 mm long. Petals 5, glabrous and reflexed, white or reportedly pale pink, oblong, rounded and often bluntly erose apically,

otherwise entire, 3–3.5 mm long, 1–1.5 mm wide. Stamens 10, isomorphic or alternately subisomorphic with larger stamens inserted on glabrous torus opposite petals and smaller stamens inserted opposite calyx lobes; filaments glabrous, complanate and constricted distally, 1.5–2 mm long; anthers 1–1.5 (–1.75) mm long and 0.5 mm wide, yellow, linear-oblong, deeply channeled

ventrally between thecae, truncate to slightly emarginate distally with a circular, somewhat dorsally inclined pore; connective simple, slightly thickened dorsally but not dilated or prolonged below thecae. Ovary inferior, 5-celled, fluted and distended apically into a glandular-puberulent, lobulate, stylar collar mostly 0.5 mm high that becomes depressed and bowl-like on maturing berries. Style straight, glabrous, 5–6 mm long; stigma truncate. Berry reportedly dark purple at maturity, globose, 6–7 mm long and 5–6 mm in diameter. Seeds numerous, galeiform to deltoid, 0.5 mm long, white or beige, irregularly angulate with a densely papillate testa and a lateral flattened or somewhat convex raphe.

ADDITIONAL SPECIMENS EXAMINED.—COSTA RICA. Cartago: Valle Escondido, 30 Mar. 1966, *Schnell* 627 (US). Heredia: Finca La Selva, OTS Field Station on Río Puerto Viejo, just E of its junction with Río Sarapiquí, 21 Jul. 1981, *Hammel* 11026 (DUKE); forest N of road to Puerto Viejo at Chilamate, 22 May 1982, *Hammel* 12423 (CAS, CR); hills near Chilamate along road between Puerto Viejo and La Virgen, 30 May 1982, *Hammel* 12668 (CAS); Chilamate de Sarapiquí, S end of Cerros Sardinal, N side of Río Sarapiquí, 10°27.5'N, 84°4'W, 3 Jul. 1985, *Hammel* & *Grayum* 14103 (CAS); Finca El Bejuco, S base of Cerros Sardinal, Chilamate de Sarapiquí, 10°27'N, 84°04'W, 2 Jun. 1985, *Grayum* & *Jacobs* 5355 (CAS); between Río Peje and Río Sardinalito, Atlantic slope of Volcan Barva, 10°18.5'N, 84°04'W, 8 Apr. 1986, *Grayum* 6910 (CAS—2 sheets); Tirimbina, 9 Jun. 1971, *Proctor* 32244 (MO). PANAMA. Bocas del Toro: between Fortuna and Chiriquí Grande, 8.5 mi [13.7 km] N of bridge over the Fortuna Lake, 08°46'N, 82°14'W, 10 Mar. 1985, *Croat* 60151 (CAS); Fortuna to Chiriquí, ca. 3 km N of continental divide, 08°48'N, 82°11'W, 12 Feb. 1986, *Hammel* & *McPherson* 14466 (CAS); Fortuna Dam region, near Chiriquí Grande, 08°45'N, 82°15'W, 18 Jan. 1986, *McPherson* 8079 (CAS); 8.5 road-miles [13.7 km] from bridge near Fortuna Dam on road towards Chiriquí Grande, 08°50'N, 82°15'W, 10 Mar. 1985, *McPherson* 6760 (CAS); road to Chiriquí Grande, 6 km N of continental divide, 08°50'N, 82°07'W, 2 Aug. 1984, *Todzia et al.* 2558 (CAS); Fortuna Dam area to Chiriquí Grande, 2 Aug. 1984, *D'Arcy et al.* 15996 (CAS); above Chiriquí Grande ca. 2 mi E on a side road ca. 10 road-miles below continental divide, 08°55'N, 82°10'W, 11 Mar. 1988, *Almeda et al.* 6082 (CAS, MO, PMA, US). Coclé: 2 mi N of Cerro Pilon, 16 Mar. 1973, *Liesner* 726 (CAS, MO); between La Junta and Limón, 5 hour walk N of Alto Calvario, 11 Oct. 1977, *Folsom* 5864 (CAS); Caribbean side of divide at El Cope, 08°45'N, 80°35'W, 4 Feb. 1983, *Hamilton & Davidse* 2776 (CAS); road from La Pintada to Coclesito, 08°45'N, 80°30'W, 7 Feb. 1983, *Hamilton & Davidse* 2815 (CAS). Colón: 9 mi [14.6 km] S of Portobello, 17 Jul. 1970, *Croat* 11372 (F, US); Río Iguanita and inland to 2 km, 7 Feb. 1981, *D'Arcy* 14615 (CAS). Darién: vicinity of gold mining camp of T. Kittredge on headwaters of Río Tuquesa ca. 2 air km from continental divide, 26 Aug. 1974, *Croat* 27210 (F); forested ridges and valleys at Mamey, 6 Mar. 1982, *Whiteford & Eddy* 374 (BM, MO). Panamá: 13 km N of El Llano on road to Cartí, 13 Feb. 1973, *Busey* 374 (US); El Llano—Cartí road, 14.8 km N of Panamanian Hwy., 27 Jan. 1977, *Folsom et al.* 1479

(MO). San Blas: Nusagandi, trail from camp NW to a quebrada, 09°19'N, 78°15'W, 31 Jul. 1984, *de Nevers & de Leon* 3595 (CAS); Nusagandi, El Llano—Cartí road, 09°19'N, 78°15'W, 10 Aug. 1984, *de Nevers & Gonzalez* 3655 (CAS); Llano—Cartí road, 19 km from Interamerican Hwy., 09°19'N, 78°55'W, 4 Sep. 1984, *de Nevers & Herman* 3831 (CAS); Llano—Cartí road, 20 km from Interamerican Hwy., 09°19'N, 78°55'W, 30 Sep. 1984, *de Nevers et al.* 3962 (CAS). COLOMBIA. Chocó: forest NW of Alto Curiche, 20 May 1967, *Duke & Idrobo* 11240 (US).

DISTRIBUTION.—Currently known from river banks, shaded sites, and light gaps in rain forests from the Puerto Viejo region of northeastern Costa Rica south through Panama to an area northwest of Alto Curiche in western Colombia, from sea level to 900 m.

PHENOLOGY.—Flowering and fruiting occur sporadically throughout the year.

Although variable in foliar size and the degree to which the elevated primaries diverge from the median nerve on lower foliar surfaces, *C. hammelii* is readily defined by the following set of characters: a divaricately branched pseudolateral inflorescence; an irregularly rupturing apiculate calyx; a fluted, glandular-puberulent stylar collar; and seeds that are galeiform to angularly deltoid in outline with a densely papillate testa. There also appears to be some intrafloral variation in staminal size among the three flowering collections available for study. A collection from Panama (*de Nevers et al.* 3962) has stamens that are alternately somewhat unequal in size (see Fig. 2), whereas *Hammel* 9682 from Costa Rica and *Todzia et al.* 2558 from Panama have stamens that are clearly isomorphic. This slight variation may prove to be taxonomically inconsequential but warrants further observation as additional flowering collections are made.

Although *C. hammelii* appears to have no close allies among described congeners, it bears a superficial vegetative resemblance to *C. reitziana* Cogn. & Gleason and *C. costaricensis* Cogn. & Gleason. Both differ from *C. hammelii* in having an adaxially pubescent torus, regularly developed (nonrupturing) calyx lobes, and smooth seeds.

A distinctive, but not always conspicuous, feature of *C. hammelii* is the occurrence of small funnel-shaped pockets or chambers in the angles between the median nerve and the base of each proximal lateral nerve (see Fig. 3). The function of these structures in any kind of symbiotic relationship is unclear. Of the numerous collections cited above, label information on only one

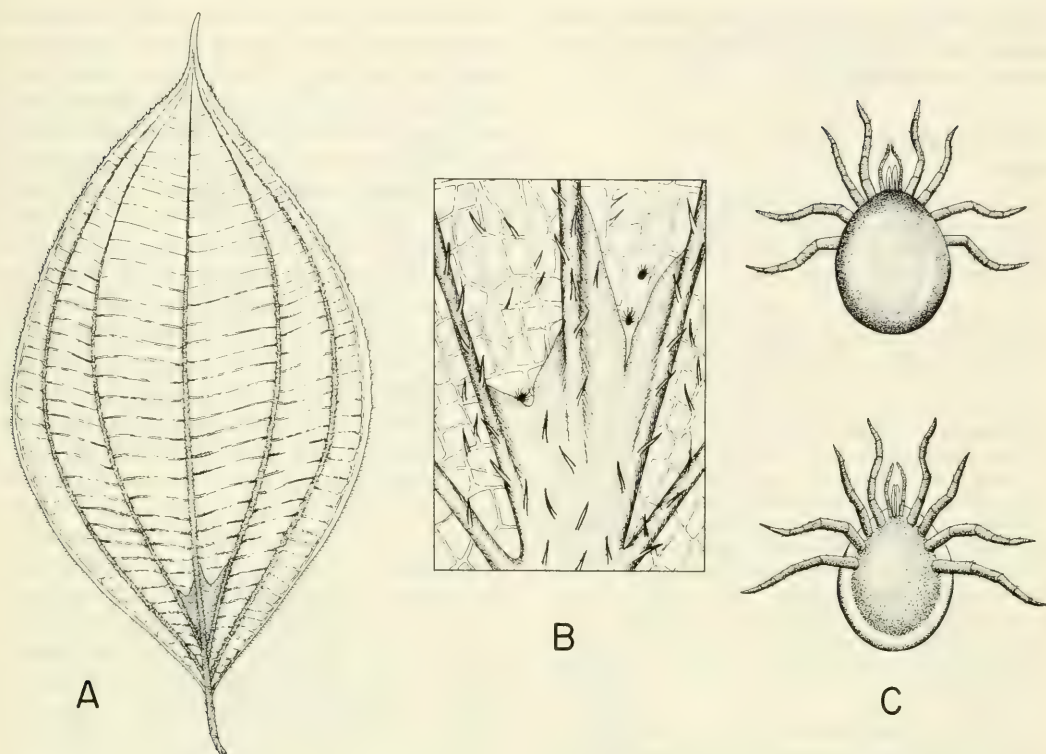


FIGURE 3. *Clidemia hammelii* Almeda. A, representative leaf (abaxial surface), $\times$ ca. $\frac{1}{4}$; B, enlargement of lower leaf surface showing pocket domatia, $\times$ ca. 5; C, the mite, *Ololaelaps* sp., dorsal view (above) and ventral view (below), $\times$ ca. 20. (A, B from Almeda et al. 6082.)

from Panama (*de Nevers & Herman 3831*) makes note of "ants in the leaves." During recent field work I examined several individuals of another Panamanian population (Almeda et al. 6082) and found mites of the genus *Ololaelaps* (Gamasida, family Laelapidae) in the domatia of at least three individuals (see Fig. 3). No other insects or arthropods, however, were encountered in the 33 domatia examined. According to G. W. Krantz (in litt., 16 June 1988) a domatium is an odd habitat for *Ololaelaps* because most are described from moss and litter substrates, or from the nests of small mammals. Because mites of this genus are thought to be predaceous, Krantz suggests that the mites may feed on resident nematodes, or they may simply use the domatia as shelters.

In his review of plant domatia, Jacobs (1966) concludes that there is no evidence to demonstrate a biological relationship between domatia-bearing plants and mites. Benson (1985), however, notes that scavenging mites are fairly

common opportunistic invaders of plant cavities. He suggests that pocket domatia, often referred to as acarodomatia, probably function as feeding sites for sucking homopterans (i.e., the coccids or scale insects, and the membracids or treehoppers). This ant-coccid linkage is intriguing when one considers that homopterans can attract ants with their honeydew secretions and gain protection from other predaceous insects. Charles Turner (pers. comm., 26 May 1988), who is currently working on mite ecology, proposes a facultative mutualistic interaction to explain the plant-mite association. He suggests that the pocket domatia may serve as egg nurseries and help to shelter the mites from predators. The mites, in turn, benefit the plant by feeding on fungal spores and the eggs of predaceous insects. The plant-mite relationship thus remains unsolved, requiring more sophisticated field-oriented study than it has received so far.

This species is named for Barry E. Hammel, a student of neotropical Clusiaceae whose col-

lecting efforts in Costa Rica and Panama have added many new and interesting plants to the flora of Mesoamerica.

***Miconia calocoma* Almeda, sp. nov.**

Figure 4

TYPE.—COSTA RICA. Heredia: Finca La Selva, OTS Field Station on Río Puerto Viejo just E of its junction with Río Sarapiquí, southeast corner, elev. 100 m, 17 Apr. 1981, *Folsom 9776* (holotype: CAS!; isotype: DUKE).

Frutex vel arbuscula 3–5 m. Ramuli teretes sicut petioli foliorum subtus venae primariae inflorescentia hypanthiaque modice pilis stellatis induti. Petioli 4–10 mm longi; lamina (4.2–)8.5–19.5 × (2.3–)5–8.5 mm elliptica vel ovato-elliptica apice acuminata basi rotundato-obtusa, 5(–7)-plinervata, membranacea et undulata vel undulato-dentata. Inflorescentia 3–7 cm longa multiflora; flores 4-meri, pedicellis (ad anthesim) 0.5 mm longis, bracteolis 2–3 mm longis anguste oblongis persistentibus. Hypanthium (ad torum) 2 mm longum; calyx primum in cono apiculato clausus demum in lobos regulares persistentes ruptus, dentibus exterioribus 1–1.5 mm eminentibus. Petala 3–4 × 1.5–2.5 mm obovato-oblonga glabra. Stamina isomorphica glabra; filamenta 1.5–2 mm longa; antherarum thecae 1–1.5 × 0.5 mm angustae oblongae, poro paulo ventraliter inclinato; connectivum nec prolongatum nec appendiculatum. Stylus 5–10 mm glaber; ovarium 4-loculare et $\frac{3}{4}$ inferum glaber.

Shrubs or small trees 3–5 m tall. Older cauline internodes terete and essentially glabrous. Distal branchlets, petioles, and inflorescences densely covered with a mixture of rusty brown sessile-stellate and stipitate-stellate hairs. Leaves of a pair typically unequal in size; petioles 4–10 mm long; blades membranaceous, (4.2–)8.5–19.5 cm long and (2.3–)5–8.5 cm wide, elliptic to elliptic-ovate, apex acuminate, base typically obtuse to broadly rounded but sometimes varying to slightly oblique at base and then somewhat decurrent on petiole, margin undulate to undulate-dentate; 5(–7)-plinerved with the inner pairs of subparallel primary nerves elevated and diverging from median nerve in opposite, subopposite, or irregularly alternate fashion at successive points above the blade base, sparingly stellate pubescent to glabrous above at maturity, copiously stellate pubescent on elevated primary nerves below with a sparser hair covering on prominulous network of transverse secondary and higher order veins. Inflorescence terminal but sometimes appearing pseudolateral because of elongation of axillary shoots, panicleiform with ultimate branchlets terminating in multiflowered, congested glomerules; bracts of rachis nodes paired, linear-oblong, 2–5 mm long, 0.5–1 mm wide, glabrous above and copiously stellate below; bracteoles persis-

tent, 2–3 per pedicel, sessile, linear-oblong, attenuate apically, 0.5–1.5 mm long, 0.25–0.5 mm wide, margin entire with a solitary apical hair, glabrous above and sparingly to moderately stellate below. Pedicels copiously stellate pubescent, 0.5 mm long but inconspicuous and concealed by congested glomerules. Hypanthia (at anthesis) campanulate, 2 mm long to the torus (vascular ring), densely stellate pubescent throughout. Calyx closed in bud and crowned by an apiculum 0.25 mm long but rupturing at anthesis into 2–4 persistent deltoid to semicircular hyaline lobes mostly 1 mm long and 1–1.5 mm wide basally; exterior calyx teeth 4, linear-oblong, 1–1.5 × 0.5 mm, copiously stellate and widely spreading to recurved on fruiting hypanthia. Petals 4, glabrous, white, obovate to oblong-obovate, widely spreading to reflexed, rounded apically, 3–4 mm long and 1.5–2.5 mm wide distally. Stamens 8, isomorphic; filaments glabrous, complanate, constricted and incurved distally, 1.5–2 mm long; anthers 1–1.5 mm long and 0.5 mm wide, yellow, linear-oblong, laterally compressed and deeply channeled ventrally between thecae, truncate to slightly emarginate distally with a somewhat ventrally inclined terminal pore; connective thickened dorsally but not dilated or prolonged below the filament insertion. Ovary ca. $\frac{3}{4}$ inferior, 4-celled, and glabrous. Style erect, often somewhat curved distally, glabrous, 5–10 mm long and conspicuously overtopping the surrounding stamens; stigma truncate to capitate. Berry reportedly blue-black to purple at maturity, globose, 6–8 mm long and 6–8 mm in diameter. Seeds numerous, obovoid to pyriform, 1 mm long, white or beige, somewhat angulate with a densely tuberculate testa and a lateral flattened raphe on the opposing face.

ADDITIONAL SPECIMENS EXAMINED.—COSTA RICA. Heredia: S of Puerto Viejo, 2 km S of Magsasay Penal Colony, W of road, 5 Feb. 1983, *Garwood et al. 1125* (BM, MO); Finca La Selva, OTS Field Station on Río Puerto Viejo, just E of its junction with Río Sarapiquí, 3,000 m line, South Boundary along Central Trail, 2 May 1981, *Folsom 9990* (CAS); Finca La Selva, OTS Field Station, South Boundary, 1,900 m E, 6 Aug. 1980, *Hammel 9452* (DUKE); Finca La Selva, OTS Field Station, South Boundary, 1,600 m E, 27 Sep. 1980, *Hammel 9872* (DUKE); Finca La Selva, OTS Field Station, South Boundary on slope just W of Q. Esquina, 15 Jul. 1982, *Hammel & Trainer 13181* (CAS). Limón: Cerro Coronel, E of Laguna Danto, 10°41'N, 83°38'W, 16–23 Jan. 1986, *Stevens 23730* (MO).

DISTRIBUTION.—A little-collected rain forest species currently known from northeastern Costa



FIGURE 4. *Miconia calocoma* Almeda. A, habit, $\times 3/4$; B, representative leaf (lower surface), $\times 3/4$; C, enlargement of lower leaf surface showing stellate pubescence; D, representative flower, $\times 12$; E, petal, $\times 10$; F, stamens, $1/4$ lateral view (left) and ventral view (right), $\times 10$; G, mature berry, $\times 4$; H, seeds, $\times 15$. (A–F from the holotype; G, H from Hammel 13181.)

Rica in an area extending from Cerro Coronel just south of Barra del Colorado southwest to the OTS La Selva Field Station and vicinity at 20–200 m.

PHENOLOGY.—Flowering and fruiting specimens have been collected from January through May and July through September, respectively.

Miconia calocoma is distinguished by its rusty stellate pubescence, 4-merous flowers, irregular-

ly rupturing apiculate calyx, unappendaged anthers, 4-celled ovary, and densely tuberculate, obovoid to pyriform seeds.

Placement of this species into Cogniaux's (1891) sectional classification depends on whether one chooses to emphasize characters of the calyx or stamens. In having oblong unappendaged stamens with ventrally inclined apical pores, *M. calocoma* would appear to belong to

section *Amblyarrhena*. Within this section, however, no particular species or group of species can be singled out as close relatives. The irregularly rupturing apiculate calyx is characteristic of section *Laceraria*, but *M. calocoma* lacks the dorsally appendiculate anthers that are typical of that section. Within this latter section, *M. calocoma* is most similar to *M. rapticalyx* Wurdack of Venezuela and *M. wagneri* Macbride of Bolivia and Peru. These two allopatric taxa share several diagnostic features with *M. calocoma* including the stellate pubescence, rupturing apiculate calyx, and 4-merous flowers. Characters that consistently separate *M. rapticalyx* from *M. calocoma* include the larger (12–28 × 9–19 cm) ovate, 5–7-nerved leaves with rounded serrulate margins, reniform bracteoles, dorsally inclined anther pores, and 2(–3)-celled ovary. *Miconia wagneri* is readily separated from *M. calocoma* by many of these same features but it differs most notably in having larger (15–25 × 8–12 cm), 5–7-nerved leaves that are entire or remotely callose-denticulate and anther connectives that are dilated at the filament insertion into dorso-basal spurs.

The epithet for this species is derived from the Greek word *kalos*, beautiful, and the Latin word *coma* (*kome* in Greek), hair tuft, in reference to the attractive covering of rusty stellate hairs on branchlets, leaves, and inflorescences.

Miconia dissitiflora Almeda, sp. nov.

Figure 5

TYPE.—COSTA RICA. Puntarenas: above Golfito along road to television tower, elev. 50–500 m, 16 Jul. 1977, *Almeda et al.* 3093 (holotype: CAS!; isotypes: BM!, BR!, CR!, DUKE!, F!, MO!, NY!, US!).

Frutex 1–3 m. Ramuli teretes sicut foliorum subtus venae primariae inflorescentia hypanthiaque sparse vel modice glanduloso-furfuracei. Folia subsessilia vel petiolis 1–5(–9) mm longis; lamina 6.5–22 × 3.1–10 cm, elliptica vel elliptico-ovata apice acuminata vel attenuata basi paulo cordata vel rotundata, 5(–7)-plinervata, membranacea et undulata vel subintegra. Inflorescentia 7–20.5 cm longa multiflora; flores 5-meri, pedicellis (ad anthesim) 1.5–2.5 mm longis; bracteolis 0.5 mm longis subulatis. Hypanthium (ad torum) 1.5 mm longum; calyx primum in cono apiculato clausus demum in lobos irregulares persistentes ruptus, dentibus exterioribus 0.5 mm eminentibus. Petala 3.5 × 1.5–2 mm oblongo-lanceolata glabra. Stamina paulo anisomorphica glabra; filamenta 1.5–2 mm longa; antherarum thecae 2 × 0.5 vel 1.5 × 0.5 mm angustae oblongae, poro paulo dorsaliter inclinato; connectivum nec prolongatum nec appendiculatum. Stylus 2.5–3 mm glaber; ovarium 5-loculare omnino inferum apice modice puberulo.

Sparingly branched shrubs 1–3 m tall. Older

cauline internodes terete and glabrous. Distal branchlets and inflorescences moderately to sparingly stellate-furfuraceous. Leaves of a pair somewhat unequal in size, typically subsessile and clasping or sometimes with petioles 1–5(–9) mm long; blades membranaceous to subcoriaceous at maturity, 6.5–22 cm long and 3.1–10 cm wide, elliptic to elliptic-ovate, apex acuminate to attenuate, base rounded to subcordate but sometimes varying to slightly oblique, margin bluntly undulate-dentate to subentire, 5(–7)-plinerved below with inner pairs of subparallel primary nerves elevated and diverging from median nerve in opposite fashion at successive points above blade base, glabrous above, glabrous to sparingly stellate on and adjacent to elevated primaries below. Inflorescence a terminal, divaricately branched paniculiform dichasium 7–20.5 × 7–30 cm; bracts of the rachis nodes paired, lance-triangular, 0.5–4 mm long, 0.5–1 mm wide, essentially glabrous throughout or sparingly stellate pubescent below; bracteoles paired, glabrous, sessile and evidently fused into a short nodal collar usually evident as an elevated interpetiolar ridge, lance-triangular to subulate, 0.5 mm long, 0.5 mm wide at base, margin entire. Pedicels sparingly stellate-furfuraceous to glabrous, 1.5–2.5 mm long. Hypanthia (at anthesis) campanulate, 1.5 mm long to torus (vascular ring), glabrous to sparingly stellulate puberulent basally. Calyx closed in bud and crowned by an apiculum ca. 0.5 mm long but rupturing irregularly at anthesis into 2–5 persistent hyaline lobes 1–1.5 mm long; exterior calyx teeth 5, subulate, 0.5 mm long, glabrous, erect to antrorsely spreading. Petals 5, glabrous, white, oblong-lanceolate, acute to retuse apically, 3.5 mm long and 1.5–2 mm wide, margin entire. Stamens 10, alternately unequal with the larger stamens inserted on the torus opposite the petals and the smaller ones inserted opposite the calyx lobes; filaments glabrous, complanate, somewhat constricted and geniculate distally, 1.5–2 mm long; anthers 1.5–2 mm long and 0.5 mm wide, yellow, linear-oblong, truncate distally with a somewhat dorsally inclined terminal pore; connective slightly thickened dorsally but not dilated or prolonged below the filament insertion. Ovary inferior, 5-celled, minutely and caducously puberulent at the summit. Style straight, glabrous, 2.5–3 mm long; stigma truncate. Berry globose, 2.5–3.5 mm long and ca. 2.5 mm in diameter. Seeds numerous, white, galeiform, 0.5 mm long with

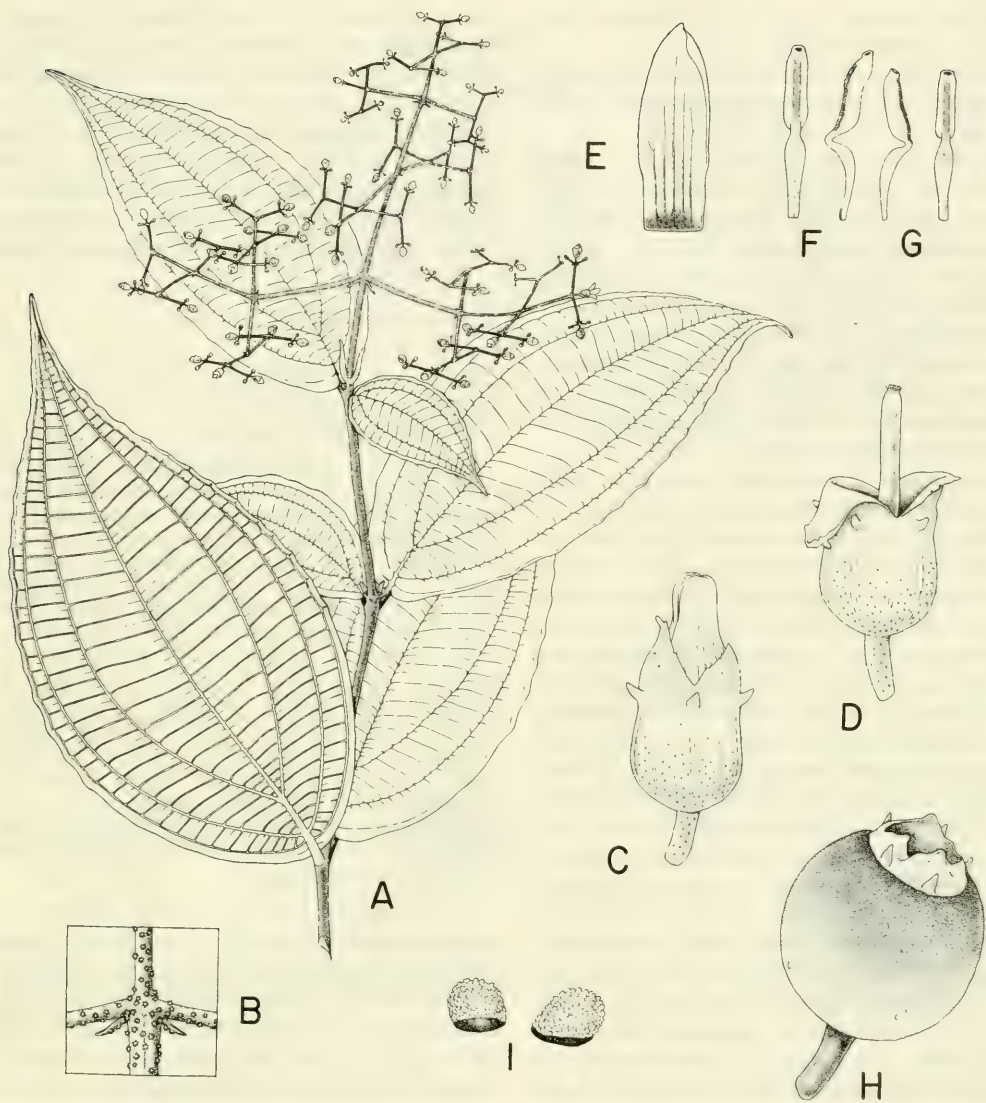


FIGURE 5. *Miconia dissitiflora* Almeda. A, habit, $\times \frac{2}{3}$; B, enlargement of inflorescence node showing bracts and stellate-furfuraceous pubescence; C, floral bud showing rupturing calyx and apiculus, $\times 12$; D, flower with petals and stamens removed, $\times 12$; E, petal, $\times 9$; F, larger (antepetalous) stamens, dorsal view (left) and lateral view (right), $\times 6$; G, smaller (antesealous) stamens, lateral view (left) and dorsal view (right), $\times$ ca. 6; H, mature berry, $\times$ ca. 10; I, seeds, $\times$ ca. 18. (A–G from the holotype; H, I from *Liesner* 2013.)

a densely muricate or verrucose testa on the convex side and a lateral raphe on the opposing face.

ADDITIONAL SPECIMENS EXAMINED.—COSTA RICA. Puntarenas: main ridge and NE slopes of Fila de Cal, between San Vito and Ciudad Neily, 08°41'N, 82°56.5'W, 13 Sep. 1985, *Grayum et al.* 6034 (CAS); NE slopes of Fila de Cal between San Vito and Ciudad Neily, 08°41'N, 82°56.5'W, 12 Jul. 1985, *Hammel & Grayum* 14187 (CAS); Rincón de Osa, Río Agua

Buena to ca. 4 km above it, 10 Feb. 1974, *Liesner* 2013 (CAS); Corcovado National Park, trail from base of hills to Los Chiles, 9 Jul. 1977, *Liesner* 3071 (CAS, CR); trail from radio tower on ridge above Golfito, opposite docks, 08°39'N, 83°10'W, 25 Jul. 1977, *Webster* 22045 (CAS).

DISTRIBUTION.—Known only from the Golfo Dulce region of southern Costa Rica in an area extending from Los Chiles in Corcovado Na-

tional Park eastward to Fila de Cal between San Vito and Ciudad Neily at 20–620 m.

PHENOLOGY.—Flowering specimens have been collected in July and September; the only fruiting specimen was collected in July.

Miconia dissitiflora is a well-defined species, readily distinguished by its sparse stellate-furfuraceous indument, divaricately branched inflorescence, irregularly rupturing calyx, unappendaged anisomorphic stamens, and oblong-lanceolate petals. It is also unusual and evidently unique among New World berry-fruited melastomes in having the larger stamens inserted on the torus opposite the petals. Among neotropical melastomes this condition is known only in the capsular-fruited genus *Monochaetum*.

The problem of placing *M. dissitiflora* into a section parallels the ambiguous situation described above for *M. calocoma*. An emphasis on staminal characters would dictate placement into section *Amblyarrhena*, whereas characters of the calyx suggest a relationship with the species of section *Laceraria*. The new species bears no strong resemblance to any of the described taxa currently placed in section *Amblyarrhena*. A search for morphologically similar species in section *Laceraria* has only served to highlight the ambiguities involved when assessing relationships based on different character sets. *Miconia centrodesma* of section *Laceraria* shares an irregularly rupturing calyx and a sparse stellate-furfuraceous indument with *M. dissitiflora*, but it differs in a number of diagnostic reproductive characters. It has 4-merous flowers, isomorphic stamens, dorsally appendiculate anthers, a 2–3-celled ovary, and narrow angular-oblong tuberculate seeds. The seeds of *M. centrodesma* are unusual in having a dilated testa at the distal end that forms a foot or spur composed of enlarged cells that collapse on drying. This “foot,” which can be observed only in fresh or hydrated material, imparts an overall shape reminiscent of a miniature boomerang. Thus, the seeds of *M. centrodesma* differ dramatically from the muricate or verrucose galeiform seeds of *M. dissitiflora*. These considerable differences suggest that the relationship between *M. centrodesma* and *M. dissitiflora* is not a particularly close one. Consequently, *M. dissitiflora* is probably best regarded as an isolated species not readily placed within the sectional classification proposed by Cogniaux (1891).

The epithet chosen for this species is derived from the Latin word *dissitus*, remote or lying

apart, referring to the well-spaced position of flowers on the divaricately branched inflorescence. It is this character, together with the small apiculate buds and plinerved leaves, that give *M. dissitiflora* an aspect reminiscent of *Conostegia cinnamomea* (Beurl.) Wurdack. The latter differs in having isomorphic stamens, a calyptriform, circumsissile calyx, and oblong, deltoid seeds that are somewhat angulate on the convex face.

Tococa croatii Almeda, sp. nov.

Figure 6

TYPE.—PANAMA. Darién: Serranía de Pirre, 9–10 km due N of Alto de Nique, elev. 1,520–1,560 m, 27 Jul. 1976, Croat 37873 (holotype: CAS!; isotype: MO!).

Frutex 0.5–1.5 m. Ramuli primum rotundato-quadrangulati demum teretes sicut foliorum venae primariae et secundariae sparse vel modice setosi pilis laevibus laxis paulo retrorsis 0.5–2 mm longis. Petioli 2.5–12.5 cm longi; lamina 12–19.5 × 8.3–15.3 cm ovata apice acuminata basi rotundata vel cordata, 7(–9)-nervata, membranacea et crenulata ciliata. Inflorescentia 10–18 cm long multiflora; flores 5-meri, pedicellis (ad anthesim) 1–4 mm longis, bracteolis 1 mm longis subulatis persistentibus. Hypanthium (ad torum) 2–2.5 mm longum; calyx primum in cono apiculato clausus demum in lobos regulares persistentes ruptus, dentibus exterioribus 0.25–0.5 mm eminentibus. Petala 5–6 × 3.5–5 mm obovata glabra. Stamina isomorphica glabra; filamenta 2.5–3.5 mm longa; antherarum thecae 1.5–2 × 1 mm oblongae inter se cohaerentes poro 0.5 mm diam.; connectivum dorsaliter ad basim dente ca. 1–1.5 mm longo descendenti armatum. Stylus 5.5–8.5 mm; ovarium 5-loculare omnino inferum apice sparsissime pilis 0.5–1 mm longis glandulosis armato.

Shrubs 0.5–1.5 m tall. Distal branchlets subquadrangular, sparsely to moderately beset with a caducous cover of straight spreading and/or somewhat crisped hairs mostly 1–2 mm long. Leaves of a pair equal to slightly unequal in size; petioles 2.5–12.5 cm long; blades thin and membranaceous, 12–19.5 cm long and 8.3–15.3 cm wide, broadly ovate to cordate, apex acuminate, base broadly rounded to cordate, margin ciliate-crenulate, 7(–9)-nerved below with all primary nerves diverging from a common point at base of blade, sparingly to moderately setulose above with smooth appressed to somewhat spreading hairs mostly 0.5–2 mm long, moderately fine setulose on and between primary nerves below with tardily caducous, simple, and glandular hairs 0.5–1 mm long. Inflorescence a terminal multiflowered panicle 10–18 cm long with subverticillate branching at secondary nodes; rachis moderately to copiously covered with spreading glandular hairs (0.5–1 mm long) and a ground layer of sessile glandular hairs; bracts of rachis nodes paired, linear-oblong, 2.5–3 mm long, 0.5 mm

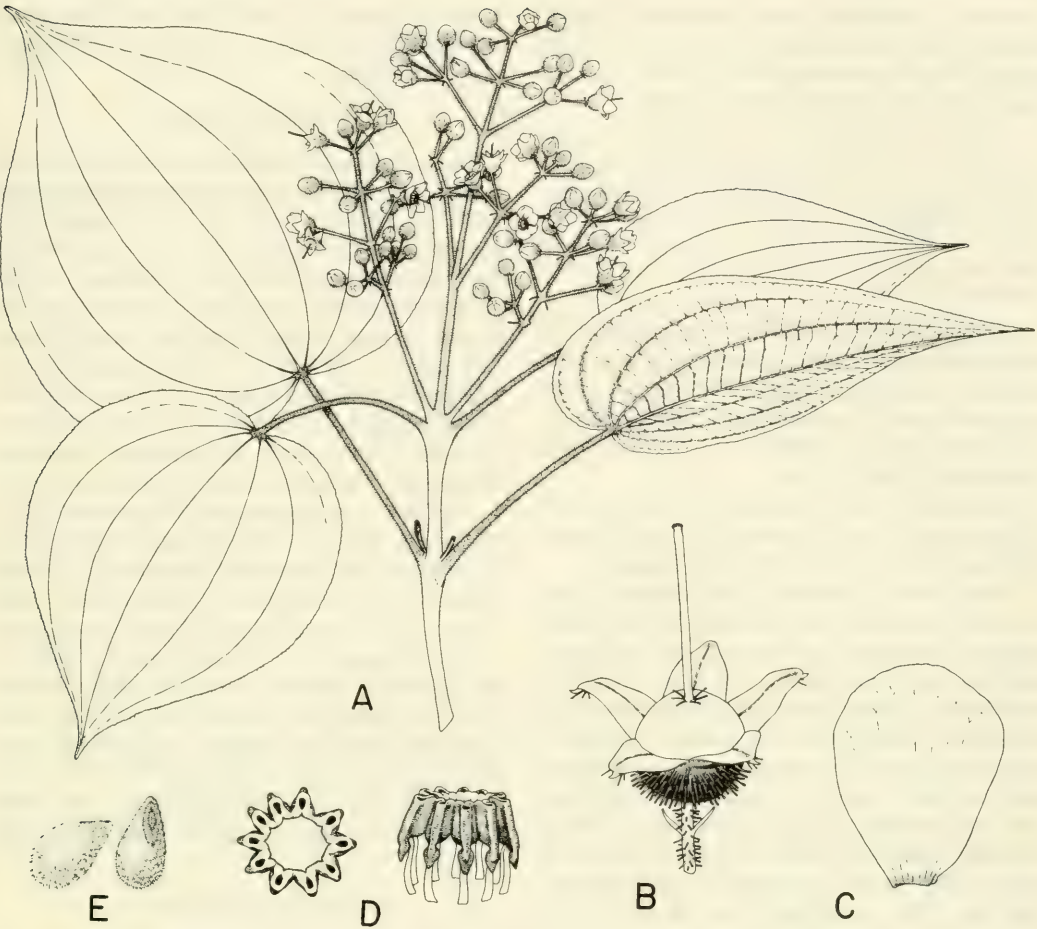


FIGURE 6. *Tococa croatii* Almeda. A, habit, $\times \frac{1}{2}$; B, flower with petals and staminal ring removed, $\times 4$; C, petal, $\times 5$; D, staminal ring as seen from above (left) and lateral view (right), $\times$ ca. 4; E, seeds, $\times$ ca. 25. (A–D from the holotype; E from Gentry & Mori 13817.)

wide, sparsely glandular setulose below intermixed with or replaced by an inconspicuous ground layer of sessile glandular hairs; bracteoles paired, sessile, and persistent, subulate to setiform, 1 mm long, essentially glabrous or with a sparse cover of sessile glandular hairs. Pedicels 1–4 mm long, beset with minute glandular hairs up to 0.5 mm long. Hypanthia (at anthesis) campanulate, 2–2.5 mm long to torus (vascular ring), moderately covered with spreading smooth glandular hairs 0.5–1 mm long intermixed with or replaced by a ground layer of sessile dot-like glandular hairs. Calyx closed in bud, crowned by an apiculum 0.5 mm long but rupturing regularly at anthesis into 5 triangular hyaline lobes 2×2 mm; exterior calyx teeth 5, fused to calyx lobes for much of their length with the free subulate

portions projecting 0.25–0.5 mm from the distal portion of each calyx lobe. Petals 5, glabrous, white (fide Croat 37873), pink (fide Hartman 12458), or bluish-purple (fide Hartman 12404), obovate, rounded apically, 5–6 mm long and 3.5–5 mm wide, margin entire. Stamens 10, isomorphic; filaments glabrous, complanate, 2.5–3.5 mm long; anthers 1.5–2 mm long, 1 mm wide, laterally compressed and coherent in a ring, apex truncate to somewhat emarginate on ventral side; connective thickened dorsally and prolonged at base into a retrorse triangular appendage 1–1.5 mm long. Ovary inferior, 5-celled, sparingly glandular-setose at summit surrounding style base. Style straight, minutely papillate distally, 5.5–8.5 mm long and conspicuously overtopping surrounding stamen ring; stigma

truncate to capitellate. Berry reportedly blue at maturity, globose, 5–6 mm long, 5–6 mm in diameter. Seeds numerous, ovoid, white, 0.5 mm long with a shallowly scrobiculate testa.

ADDITIONAL SPECIMENS EXAMINED.—PANAMA. Darién: Cerro Mali, vicinity of base camp, 1,400 m, near Colombian border, 23 Jan. 1975, *Gentry & Mori 13817* (F, US); SW ridge leading to Alturas de Nique on border with Colombia, 1,100–1,200 m, 30 Dec. 1980, *Hartman 12404* (CAS); Alturas de Nique and ridge leading SW, 1,250–1,500 m, 31 Dec. 1980, *Hartman 12458* (CAS).

DISTRIBUTION.—A little-collected species of eastern Panama currently known from Cerro Mali in the Serranía del Darién and the region of Alturas de Nique in the Serranía de Pirre in southern Darién province near the Panama/Colombia frontier at 1,100–1,560 m.

PHENOLOGY.—Flowering specimens have been collected in July and December; the only known fruiting specimen was collected in January.

Tococa croatii is defined by its caducous cover of straight or crisped cauline hairs (1–2 mm long), regularly rupturing hyaline calyx, and shallowly scrobiculate, ovoid seeds. The most extraordinary feature of this species is the morphology of the anther thecae. These are distally truncate to emarginate with a comparatively broad terminal pore, laterally coherent in a ring, and beset dorsally with deflexed triangular appendages. Among described species of *Tococa*, *T. croatii* shares its habit, inflorescence architecture, staminal details, and fruit morphology only with *T. symphyandra* (Triana) Cogn. of Colombia and Ecuador. The consistent differences between these species involve foliage characters and pubescence details of the distal internodes, hypanthia and ovaries. *Tococa symphyandra* has long subtrorse-setose hairs (0.5–1.5 cm long) on young branchlets and petioles, didymous formicaria about 1 cm long that are immersed in the blade base, and essentially glabrous hypanthia and ovaries. The derived staminal characters that unite *T. croatii* and *T. symphyandra* as a distinctive species pair are also the features that make them anomalous members of the genus. These staminal characters would also make them equally anomalous if included in *Miconia* or any other genus of the Miconieae. Consequently, the precise relationships and best generic disposition for these two species must await detailed monographic studies of both *Miconia* and *Tococa*.

This species is named for Thomas B. Croat, a student of neotropical Araceae who has contrib-

uted significantly to our knowledge of the neotropical flora through his many fine collections and publications.

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SYSTEMATIC REVISION AND DESCRIPTION OF NEW
SPECIES OF SUCKERMOUTH CATFISHES
(*CHILOGLANIS*, MOCHOKIDAE)
FROM CAMEROUN

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ABSTRACT: Ten species of *Chiloglanis* occur in Cameroun: *C. batesii* Boulenger, 1904 (all or almost all river basins); *C. benuensis* Daget and Stauch, 1963 (Niger); *C. cameronensis* Boulenger, 1904 (Lokunje, Kribi, Kienke, Ntem); *C. disneyi* Trewavas, 1974 (Mungo and Cross); *C. harbinger* new species (Lokunje); *C. niger* new species (Niger); *C. polypogon* new species (Cross); *C. reticulatus* new species (Congo); *C. sanagaensis* new species (Sanaga); and *C. voltae* Daget and Stauch, 1963 (Niger).

Chiloglanis disneyi, *C. harbinger*, *C. niger*, *C. polypogon*, and *C. sanagaensis* are known only from Cameroun; *C. benuensis* occurs in the River Benue in Cameroun and Nigeria. *Chiloglanis reticulatus* also occurs in the Congo basin in northwestern Zaire. *Chiloglanis batesii* (including its synonym *C. micropogon* Poll, 1952) occurs in suitable habitats throughout the Niger and Congo basins, and is the only species of *Chiloglanis* known from the Chad basin. *Chiloglanis cameronensis* is the only species known in the Ogooué basin (Gabon). *Chiloglanis voltae* is also known from the Benue in Nigeria and the Volta basin (Ghana and Burkina Faso).

In all of the major river systems of Cameroun two or even three species of *Chiloglanis* occur sympatrically. Sympatric species usually differ strongly in sucker morphology, number and length of barbels, dentition, coloration, adult size, and other characteristics. Secondary sexual dimorphism is marked in some species, apparently absent in others.

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INTRODUCTION

Chiloglanis belongs to the endemic African catfish family Mochokidae. Adults range in size from about 18 to 100 mm standard length. The sucker or oral disc is formed by the enlarged upper and lower lips. The maxillary barbels lie free at the sides of the upper lip but the mandibular or mental (chin) barbels are largely incorporated into the lower lip.

A total of 34 species of *Chiloglanis* has been recognized, of which six have been reported from Cameroun: *C. batesii* Boulenger, 1904; *C. ben-*

uensis Daget and Stauch, 1963; *C. cameronensis* Boulenger, 1904; *C. disneyi* Trewavas, 1974; *C. micropogon* Poll, 1952; and *C. voltae* Daget and Stauch, 1963. For a review of the literature on species of *Chiloglanis* and their distribution see Daget et al. (1986). Two recent papers have dealt with *Chiloglanis* from parts of Cameroun: the Camerounian portion of the Benue (Niger basin) by Daget and Stauch (1963), and the Mungo and Meme, small coastal streams in western Cameroun, by Trewavas (1974). The results of these studies and my interpretations of them are incorporated in the present paper.

Most species of *Chiloglanis* are represented in museum collections by only a few specimens, often in poor condition. In 1980 I travelled extensively in Cameroun, collecting in the Niger, Ndian, Cross, Sanaga, and Congo basins. Additional collections were made in Cameroun in 1987–88. Specimens of *Chiloglanis* were collected readily with a nylon flyscreen pushnet in rocky substrate, gravel bars, and sand riffles. This resulted in discovery of four undescribed species. An additional new species, from the Lokunje basin, was discovered in the fish collection of the California Academy of Sciences. I visited the Lokunje in December 1987 but was unable to collect additional specimens. Five of the six species previously reported from Cameroun are recognized as valid. After study of over 40 lots and nearly 2,000 specimens referable to *C. batesii* and *C. micropogon*, including type specimens, I regard *C. micropogon* as a junior synonym of *C. batesii*. *Chiloglanis batesii* is perhaps the most widely distributed species of *Chiloglanis*. It occurs in suitable habitat in all or almost all river basins of Cameroun, throughout the Niger and Zaire basins, and is the only species of the genus in the Chad basin; it is absent west of the Niger basin. *Chiloglanis disneyi*, hitherto known only from the Mungo, is reported from the Cross basin. The new species described from Cameroun are: *C. niger* (Niger basin); *C. poly-pogon* (Cross); *C. sanagaensis* (Sanaga); *C. har-binger* (Lokunje); and *C. reticulatus* (Congo). The first four are known only from Cameroun. The fifth is also present in the Congo basin in Zaire.

Little is known about the biology of *Chiloglanis* or of any other mochokids. At least some species of *Chiloglanis* have surprisingly large eggs. Ovarian eggs of 1.7 and 1.9 mm were reported in *C. batesii* of 28 and 35.5 mm, respectively, by Trewavas (1974:363). A 37.2 mm specimen from Kivu has ovarian eggs of 2.0 mm. The total number of eggs in this specimen is at least a dozen, but no more than 20 (all but one or two have been left in situ). The holotype of *C. reticulatus* is a gravid female with about 40 eggs to 1.8 mm. In *C. batesii* and in *C. reticulatus*, ripe ovaries contain several size classes of eggs. Sexually mature males of all species have lobate testes, which in very ripe individuals may cause abdominal expansion comparable to that caused by enlarged ovaries of gravid females. In several species males have an elongate genital papilla, the functional

significance of which is unknown. Males of a few species have the humeral process of the pectoral girdle greatly enlarged, but the significance of this is also unknown. *Chiloglanis* feed mainly on insects and attached algae. The species differ strikingly in dentition and other morphological features related to feeding, but these differences have not been correlated with particular foods.

STUDY MATERIAL

Material examined is deposited in the following institutions (standard symbolic codes from Leviton et al. 1985): BMNH, British Museum of Natural History; CAS and CAS-SU, California Academy of Sciences; FMNH, Field Museum of Natural History (Chicago); MCZ, Museum of Comparative Zoology; MHNG, Muséum d'Histoire Naturelle, Genève; MNHN, Muséum National d'Histoire Naturelle; MRAC, Musée Royal de l'Afrique Centrale (Tervuren); UMMZ, Museum of Zoology, University of Michigan; and USNM, Smithsonian Institution.

Camerounian and non-Camerounian material of species of *Chiloglanis* found in Cameroun is listed in the systematic account of each species.

The abbreviation "R.", always placed in front of the proper name, stands for River, rivière, Río (Spanish), and rio (Portuguese). I have adopted this practice when writing on African freshwater fishes because the same river is often shared by two or more English-, French-, Spanish-, or Portuguese-speaking countries; authors in French usually refer to any river, regardless of what country it is in, as "rivière," while authors in English use "River"; and although in English the word "River" may precede or succeed the proper name, in the other languages the word for river always precedes the proper name.

The following comparative material of non-Camerounian species of *Chiloglanis* and of the suckermouthed mochokid genera *Atopochilus* and *Euchilichthys* has been examined:

- Chiloglanis brevibarbis* Boulenger, 1902: MHNG 2000.68-82, 15: 29.3–57.7 mm, Kenya, R. Athi at Kabaa.
- Chiloglanis congicus* Boulenger, 1920: CAS(SU) 66706, 51.6 mm, Congo basin, probably Stanley Pool; CAS 44887, 2: 58.0–59.5 mm, aquarium specimens; CAS 60812, 60.7 mm, Congo basin, R. Inkisi below Chute de Sanga.
- Chiloglanis deckenii* Peters, 1868: MHNG 1443.79-83, 5: 25.8–33.4 mm, Kenya, R. Kerio near Tambach.
- Chiloglanis neumanni* Boulenger, 1911: UMMZ 199975, 199988, and 200183, 19: 19.5–40.8 mm, Zambia, Luapula-Congo basin.

- Chiloglanis niloticus* Boulenger, 1900: MNHN 1907-230, 39.4 mm, R. Nile at Arko, Sudan (syntype).
- Chiloglanis occidentalis* Pellegrin, 1933: UMMZ 182016, 24.0 mm, tributary of R. Senegal; CAS(SU) 62926, 56: 19.9–40.5 mm, Ghana, R. Ankwa; CAS(SU) 62927, 4: 30.7–46.4 mm, Ghana, Opon Valley; CAS(SU) 62928, 56.7 mm, Ghana, R. Ahiri near Wasa Akropong; MCZ 48063, 25.6 mm, Ghana, Pra basin, Tiwifu Prasu; V. G. F. Smith collection, uncat., 26.4 mm, Nigeria, Niger basin, R. Lere, Jos Plateau; BMNH 1935.5.29:52, 18.8 mm, Nigeria, Niger basin, R. Kaduna.
- Chiloglanis polyodon* Norman, 1932: BMNH 1901.12.26, Sierra Leone, headwaters of R. Bagbwe (holotype).
- Chiloglanis sardinhai* Ladiges and Voelker, 1961: USNM 265443, 5: 28.1–37.1 mm, Angola, Benguela, Caibambo.
- Atopochilus savognani* Sauvage, 1878: CAS(SU) 15715, Cameroun, R. Niem, Nyabessan.
- Atopochilus* sp. undet. a: CAS(SU) 64793, 98.2 mm, Congo basin, Stanley Pool.
- Atopochilus* sp. undet. b: CAS 60815, 31.5 mm, Congo basin, R. Lufu.
- Euchilichthys dybowskii* (Vaillant, 1892): MNHN 1892-81, 34.0 mm, Congo basin, Oubanghi (syntype); MCZ 48356, 5: 40.8–63.2 mm, Congo basin, R. Mbomou at Gozobangui.
- Euchilichthys royauxi* Boulenger, 1902: CAS(SU) 64612, 2: 89.6–175 mm, Congo basin, rapids of lower Congo at Kinshuka.

Characters Useful in Distinguishing Species of *Chiloglanis*

Apart from Trewavas (1974), almost no authors have given adequate discussion or definitions of the characters used to define species of *Chiloglanis*. Some easily observed features of the sucker and dentition have not been utilized, and discussion of variation with age or sex is generally lacking. Observation of previously unobserved or unreported features, such as tubercles and taste buds, is facilitated by scanning electron microscopy. Some useful characters, none previously utilized, can be observed in radiographs.

SUCKER AND BARBELS.—All species of *Chiloglanis* have a well-developed sucker or oral disc (Fig. 1), made of the greatly expanded and united upper and lower lips. The lower lip incorporates much or almost all of the mental (mandibular or chin) barbels. The most obvious differences in the sucker of various species involves the mental barbels. In some species they project considerably from the posterior border of the lower lip, in others they project moderately, and in still others slightly or not at all. Some species have only two prominent mental barbels on each side of the lower lip. These correspond to the primary or primitive pair of mental barbels found in almost all groups of catfishes. In other species there are up to five auxiliary mental barbels on each

side of the lower lip. In most species with auxiliary mental barbels, these occur inside the outer primary mental barbel, but one species (*C. polypogon*) usually has an auxiliary mental barbel external to the outer primary mental barbel. Camerounian species of *Chiloglanis* with mental barbels projecting considerably from the lower lip (i.e., with “large” mental barbels) are *C. benuensis*, *C. polypogon*, *C. reticulatus*, and *C. voltae*. *Chiloglanis reticulatus* and *C. voltae* have only primary mental barbels, while *C. benuensis* and *C. polypogon* have well-developed auxiliary mental barbels. *Chiloglanis voltae* is unique in having very elongate outer mental barbels and very short inner ones. Species with mental barbels projecting very little (“minute” mental barbels) are *C. batesii*, *C. disneyi*, *C. harbinger*, and *C. niger*. *Chiloglanis camerounensis* and *C. sanagaensis* have moderately projecting mental barbels.

Other obvious differences between species involve size and shape of the sucker. In some species it is transversely oval (i.e., broader than long) and relatively (proportionately) small compared to the size of the fish, e.g., in *C. benuensis*, *C. polypogon*, and *C. reticulatus*. In others it is relatively round, e.g., *C. disneyi*, *C. harbinger*, and *C. niger*. The last two species have perhaps the largest suckers of any species of *Chiloglanis*. The papillae on the sucker also differ among species. In *C. benuensis*, *C. polypogon*, and *C. reticulatus* they are especially large, particularly on the median part of the lower lip. In *C. voltae* the papillae are greatly reduced or absent. In *C. sanagaensis* they are extremely numerous, evenly distributed and of nearly the same size over virtually the entire sucker. In all species the two halves of the lower lip are separated distally by a median cleft. In most species the cleft is very deep, so that most of the median papillate area of the lower lip is also cleft, but in *C. niger* the cleft is shallower and the median papillate area undivided. The boundary between upper and lower lips is relatively well defined in some species, e.g., *C. benuensis*, *C. polypogon*, and *C. reticulatus*, but is indistinguishable in others, e.g., *C. niger*. The upper lip of *C. disneyi* extends posteriorly under the lower and is broadly fused to it, but retains a free posterior margin where it has joined the lower lip.

Each half of the lower lip has two medullary cartilages. Difficult to see in some species or spec-

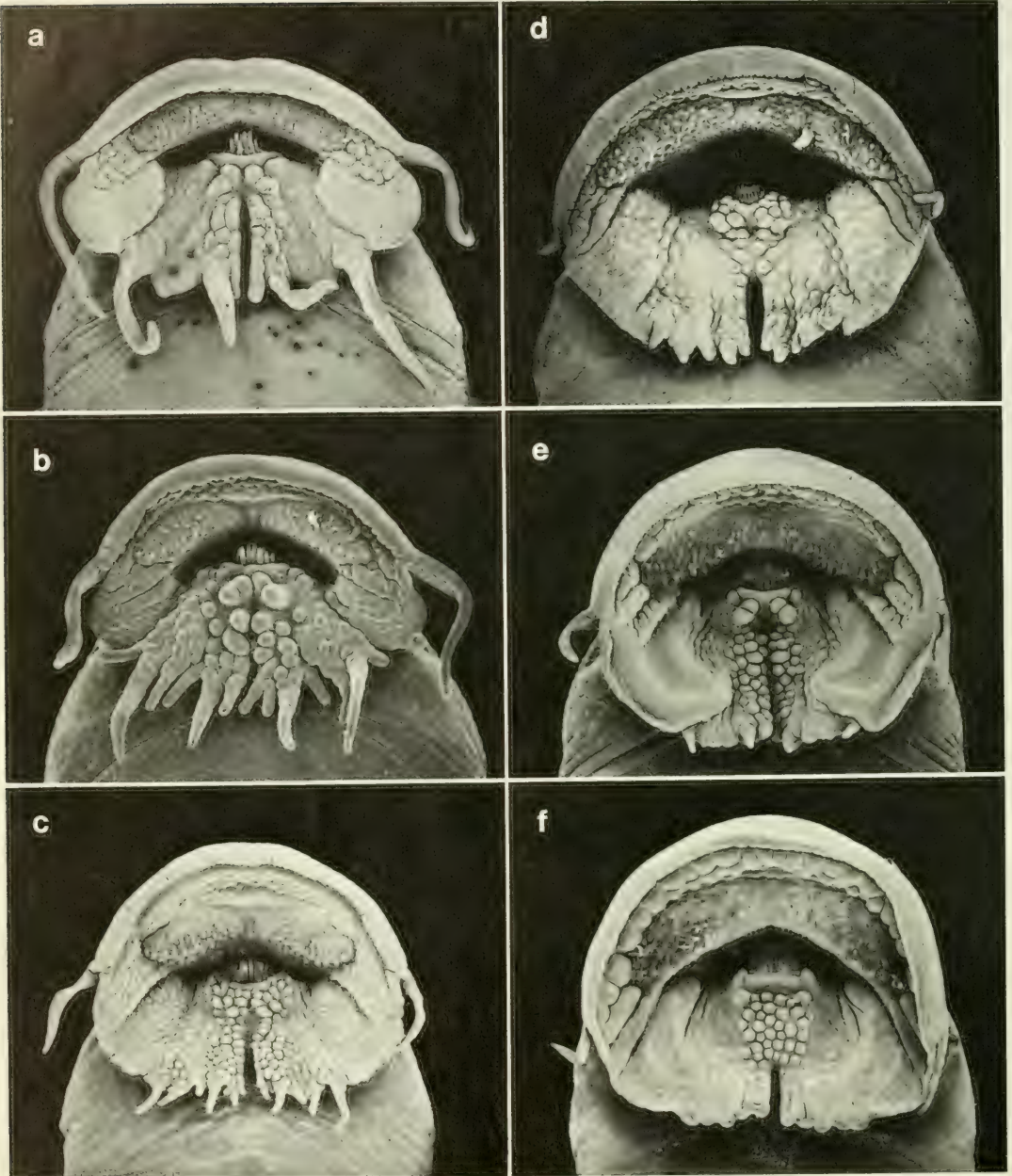


FIGURE 1. Suckers of Camerounian species of *Chiloglanis*. a, *C. reticulatus*, 31.3 mm paratype (Congo basin); b, *C. polypogon*, 25.0 mm paratype (Cross basin); c, *C. sanagaensis*, 28.6 mm paratype (Sanaga basin); d, *C. batesii*, 21.7 mm (Sanaga basin); e, *C. disneyi*, 23.0 mm (Cross basin); f, *C. niger*, 27.8 mm paratype (Niger basin).

imens, in others they are large, naturally reddish or purplish, and readily observed with transmitted light. The distal portion of each medullary cartilage typically is trifurcate; occasionally a cartilage may have four branches (see Trewavas

1974:360–361, fig. 5a). The branches of the medullary cartilages are longest in species with large barbels. In *C. reticulatus* and *C. voltae*, which have no auxiliary mental barbels, the medullary cartilages are nevertheless tri- or quadrifurcate.

The large central branch of each medullary cartilage lies in the middle of a primary mental barbel and extends almost to its tip. The lateral branches, much shorter than the central one, extend along the lateral margins of the portions of the disc projecting posteriorly between the bases of the barbels. In *C. polypogon*, in which the portions of the disc between the primary mental barbels are greatly prolonged as auxiliary mental barbels, a lateral branch of the medullary cartilage lies in the center of each auxiliary barbel.

DENTITION.—The dentition of *Chiloglanis*, like that of most mochokids, is highly specialized, and its description has given rise to much confusion. As in *Synodontis*, the mochokid genus with the largest number of species, the teeth are S-shaped. An exception is provided by *C. voltae*, in which the teeth are almost straight. The morphology of the teeth has been described and illustrated for many species of *Synodontis* (Poll 1971), but this has not been done for *Chiloglanis*. The premaxillary (upper jaw) teeth are of two sizes, large and small. The large teeth are arranged in two oval patches, one on each premaxillary, separated by a toothless median gap. The teeth in these patches form somewhat irregular rows that nevertheless can be counted; the number varies from two to eight. Most species have three to five rows, *C. batesii* and *C. disneyi* three or four, *C. harbinger* to seven, *C. niger* to seven or eight; *C. voltae* only two. In addition to the oval patches of large teeth, the upper jaw bears numerous small teeth forming a shallowly V-shaped series across the angle of the upper jaw where the flat external surface bearing the oval patches curves sharply upwards toward the roof of the mouth. Some of these teeth are firmly implanted on the premaxillary bones, while others lie more or less loose in the membrane between the premaxillary bones. The innermost or most posterior row of teeth in this series may be somewhat longer and more slender, forming a row of ciliiform teeth (sensu Trewavas 1974:359 et seq.). This tooth row, while it varies in prominence and degree of differentiation from the rest of the small premaxillary teeth, is present in most species of *Chiloglanis*. According to Trewavas (1974:358–359) the disposition of small premaxillary teeth differs in *C. batesii* and *C. micropogon*: “in *C. batesii* the attached and free teeth compose a uniform group, but in *C. micropogon* the median teeth are still smaller and

sections show that the membrane in which they lie forms a minute pouch opening backwards, the teeth at the edge of the pouch forming a transverse series across the midline. Examined with a dissecting microscope, these latter appear as a row of minute ciliiform teeth on a small membranous curtain.” This lengthy quote provides the best account of a peculiar feature of the dentition of *Chiloglanis*, and purportedly as a basis for distinguishing *C. batesii* and *C. micropogon*. My observations suggest that a complete row of ciliiform teeth is characteristic of most species of *Chiloglanis* except *C. voltae*. In many freshly preserved specimens identified by me as *C. batesii*, the ciliiform teeth are highly visible, and the membranous pouch described by Trewavas is fully evident. In other specimens, including some collected by Bates at Efulen (type locality of *C. batesii*), they appear at first glance to be absent. However, in at least some of these specimens the delicate membrane bearing the ciliiform teeth is shrunken and collapsed against the roof of the mouth, so that the teeth no longer project normally downwards. In this connection it may be noted that a small specimen from the R. Lobi in Cameroun, originally identified as *C. batesii* by Boulenger, was re-identified as *C. micropogon* by Trewavas (1974:361), and that part of the type series of *C. batesii* was collected in tributaries of the Lobi. It may also be noted that in another species, *C. brevibarbis*, Trewavas (1974:364) reported ciliiform teeth present in only one specimen among several she examined.

The mandibular or lower jaw teeth, arrayed in a relatively small area near the symphysis of the lower jaw in all species of *Chiloglanis* except *C. voltae*, usually comprise an internal row of functional teeth and an external row (rarely two or three external rows) of replacement teeth (Fig. 2). In most species the teeth in the replacement row erupt nearly simultaneously, so that depending upon the stage in the replacement cycle, teeth of the lower jaw are either in only a single row (the functional row) or in two rows (functional and replacement). This simple situation may be complicated when the row of functional teeth has been shed or only partially shed, and only part of the replacement tooth row has moved into functional position. In some species, especially those with numerous teeth such as *C. disneyi*, *C. harbinger*, and *C. niger*, the replacement process tends to be very regular, and it seems

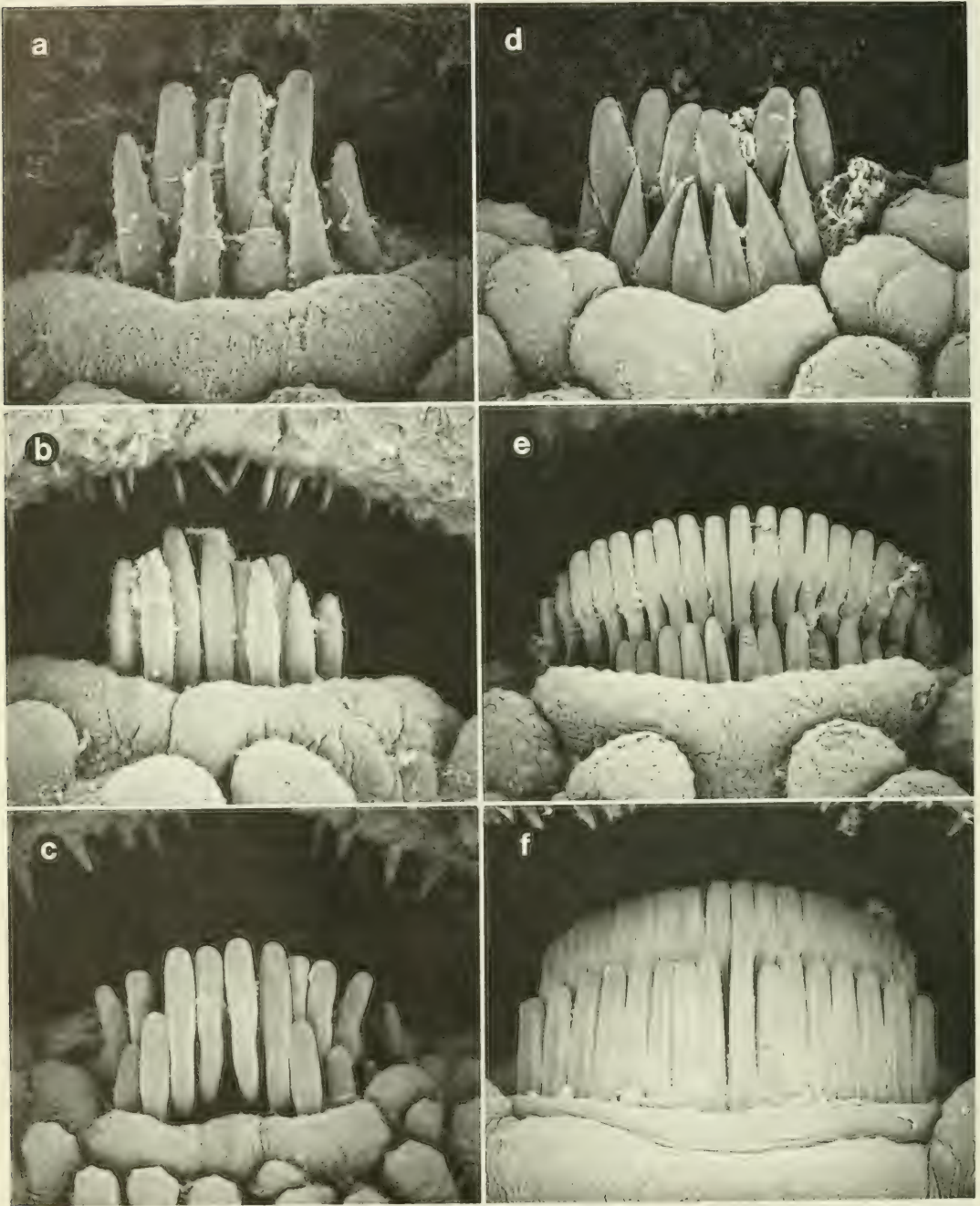


FIGURE 2. Mandibular teeth of Camerounian species of *Chiloglanis*. a, *C. reticulatus*, 31.3 mm paratype; b, *C. polypogon*, 25.0 mm paratype; c, *C. sanagaensis*, 28.6 mm paratype; d, *C. batesii*, 21.7 mm; e, *C. disneyi*, 23.0 mm; f, *C. niger*, 27.8 mm paratype.

that an old row of functional teeth is shed nearly simultaneously or as a unit, to be replaced at once by a complete row of replacement teeth. In others, e.g., *C. polypogon* and *C. congicus*, it seems that those near the symphysis fall out first, to be

replaced by corresponding teeth from the replacement row before the more lateral functional teeth are shed. The sequence of tooth replacement has not been investigated in detail.

In *Chiloglanis* generally, allowing for individ-

ual variation due to loss or injury of teeth and irregularities in replacement, there are basically two rows of mandibular teeth, an internal functional row and an external replacement row; the number of teeth of the left and right side of the lower jaw is usually equal. The number of teeth in the replacement row usually corresponds to that in the functional row. There is some increase in number of teeth with growth, but throughout the size range of specimens examined for this report, the ontogenetic increase does not amount to more than four to six functional mandibular teeth even in species with the highest tooth counts. In numerous specimens of *C. batesii*, the functional tooth row has 6 teeth on the left side and 6 on the right, and the replacement tooth row has the same count. Thus, the basic number of mandibular teeth in this species usually is 6+6. Although some specimens of *C. batesii* have fewer than 6+6 (usually 5+5 or 4+4) I have not observed any with more than 6+6.

Species of *Chiloglanis* previously reported to have numerous mandibular teeth are *C. congicus*, *C. disneyi*, *C. lamottei* Daget, 1948, *C. marlieri* Poll, 1952, and *C. polyodon*. These were discussed in connection with the description of *C. disneyi* by Trewavas (1974:365–367). *Chiloglanis congicus* has mandibular teeth tightly bunched together (“en bouquet”). The teeth near the symphysis (middle of the bouquet) have their crowns projecting more than those at the sides. Trewavas gave the mandibular tooth count as 18 but did not explain how the count was made. In four specimens of *C. congicus* I find the total number of mandibular teeth is 12, 16, 16, and 19. In the first three specimens there are basically two rows of teeth (one functional, one replacement) with 4+4 or 5+5 teeth in each row. The fourth specimen has two or three rows of teeth, one functional and one or two replacement, with the rows deranged and some teeth missing. On each side of any of the rows the maximum number of teeth is 4. *Chiloglanis lamottei*, known only from the holotype from the R. Cavally, has a single row of 14 mandibular teeth (Daget 1948), presumably 7+7. *Chiloglanis polyodon*, known only from the holotype from the R. Bagbwe, was originally described as having mandibular teeth “arranged in two parallel rows, each consisting of 15 or 16 teeth, those of the inner row larger and more curved than those of the outer (Norman 1932:184). Some 40 years later the holotype was re-examined and found to have 15 inner and 14 outer mandibular teeth bunched together”

TABLE 1. Mandibular tooth counts in species of *Chiloglanis*.

<i>C. polypogon</i>	3+3 or 4+4
<i>C. reticulatus</i>	3+3 to 5+5?
<i>C. congicus</i>	4+4 (occasionally 5+5?)
<i>C. sanagaensis</i>	4+4 or 5+5 (rarely 6+6)
<i>C. benuensis</i>	3+3 to 6+6
<i>C. cameronensis</i>	4+4 to 8+8
<i>C. batesii</i>	4+4 to 6+6
<i>C. lamottei</i>	7+7
<i>C. polyodon</i>	7+7 to 8+8
<i>C. disneyi</i>	8+8 to 10+10
<i>C. niger</i>	8+8 to 10+10
<i>C. marlieri</i>	13+13 (or 14+14?)
<i>C. harbinger</i>	13+13 to 15+15

(Trewavas 1974:367). Both accounts are cited here because of the possibility that in the intervening period a tooth was removed from each row, possibly by Norman himself. The basic mandibular tooth count for *C. polyodon* presumably is 7+7 or 8+8. *Chiloglanis marlieri* is known only from the holotype collected in the R. Nda-kirwa, a tributary of the R. Lowa, west of Lake Kivu. As originally illustrated this specimen has one complete mandibular tooth row of 15+15 teeth, plus an incomplete internal row with 7 teeth on the extreme left side, 8 on the extreme right, and none in the large intervening space (Poll 1952:227, fig. 2). Trewavas (1974) re-examined this specimen and reported the mandibular teeth as “one row of 26, a widely interrupted row of 6+7 and 2 incompletely erupted teeth at the midline.” Thus the basic tooth count presumably is 13+13 or 14+14. Mandibular tooth counts for various species of *Chiloglanis* are presented in Table 1.

TASTE BUDS.—Taste buds (Figs. 3, 4) were reported (not figured) on the papillae or “bosses of thickened epithelium” on the oral disc of *C. batesii* and *C. micropogon* (regarded here as a synonym of *C. batesii*) by Trewavas (1974). I have observed taste buds with scanning electron microscopy in one or two specimens of five species from Cameroun, and failed to find them in specimens of a sixth (Figs. 3, 4). The following remarks are presented as generalizations on the taste buds of these six species, but the limited number of specimens on which they are based should be kept in mind. The buds are largest and most abundant in *C. polypogon* and *C. reticulatus*. In these species they are distributed fairly uniformly on the papillae and barbels of the lower lip. In *C. reticulatus* the buds are about 50 μ m diameter, and the sensory field (with numerous

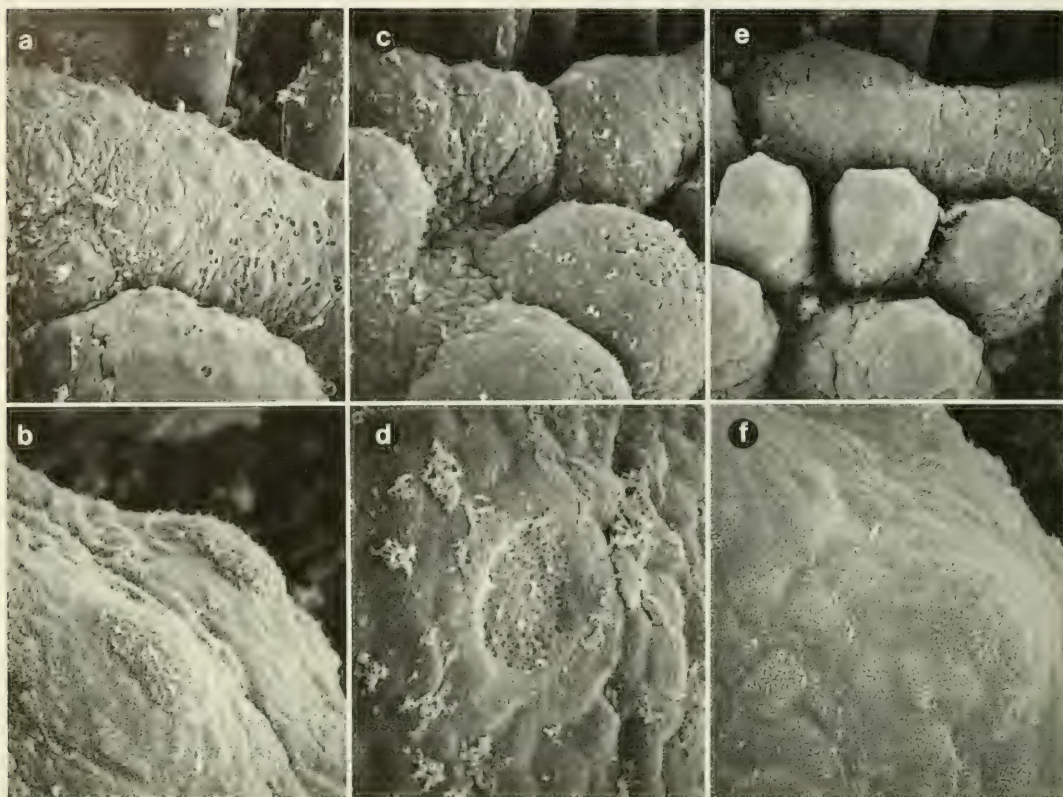


FIGURE 3. Taste buds in Camerounian species of *Chiloglanis*. a, b, *C. reticulatus*, 31.3 mm; c, d, *C. polypogon*, 25.0 mm; e, f, *C. sanagaensis*, 28.6 mm. Horizontal field widths: a, c, e (top row) = 450 μ m; b, d, f (bottom row) = 45 μ m.

minute pores for the sensillae) of each bud is about 18 μ m diameter. The sensory field projects from the summit or apex of the taste bud (Fig. 3b). The density of the taste buds, calculated from Figure 3b, is about 240 per square mm; this is about the same as that reported for taste buds in the mouth and pharynx of the common Eurasian loach *Cobitis taenia* Linnaeus, 1758 by Jakubowski (1983:850). The taste buds and sensory fields of *C. polypogon* are of about the same size, but the sensory field tends to be sunken into the middle of the bud rather than elevated (Fig. 3d). A similar condition is reported for the external taste buds of *Cobitis taenia* by Jakubowski (1983:851, fig. 1D) but has not been observed in other *Chiloglanis*. *Chiloglanis disneyi* has relatively large, numerous buds on the lower lip. The buds are up to 22 μ m diameter and the sensory fields to 7 or 8 μ m diameter (Fig. 4d). Slightly larger buds occur in *C. batesii* (Fig. 4b). Extensive viewing of the sucker of *C. niger* with SEM re-

vealed no large or well formed taste buds. Only a few small structures tentatively identified as taste buds were observed on papillae on the lower lip (Fig. 4f). The largest bud is 12 μ m diameter with a sensory field of about 8 μ m diameter. The sensory field has fewer pores than observed in other species of *Chiloglanis*. Taste buds apparently are absent in *C. sanagaensis*. I could not find any on the sucker of a 28.6 mm specimen. Although the oral papillae of this specimen have raised areas similar to those where taste buds occur in other species, their summit is occupied only by densely convoluted microvillar ridges, without any sensillar pores. The structures superficially most similar to taste buds observed in *C. sanagaensis* are illustrated in Figure 3e, f).

The species of *Chiloglanis* with the largest and most numerous taste buds, *C. polypogon* and *C. reticulatus*, have suckers with large barbels and large papillae. Taste buds of intermediate size and abundance occur in *C. batesii* and *C. disneyi*,

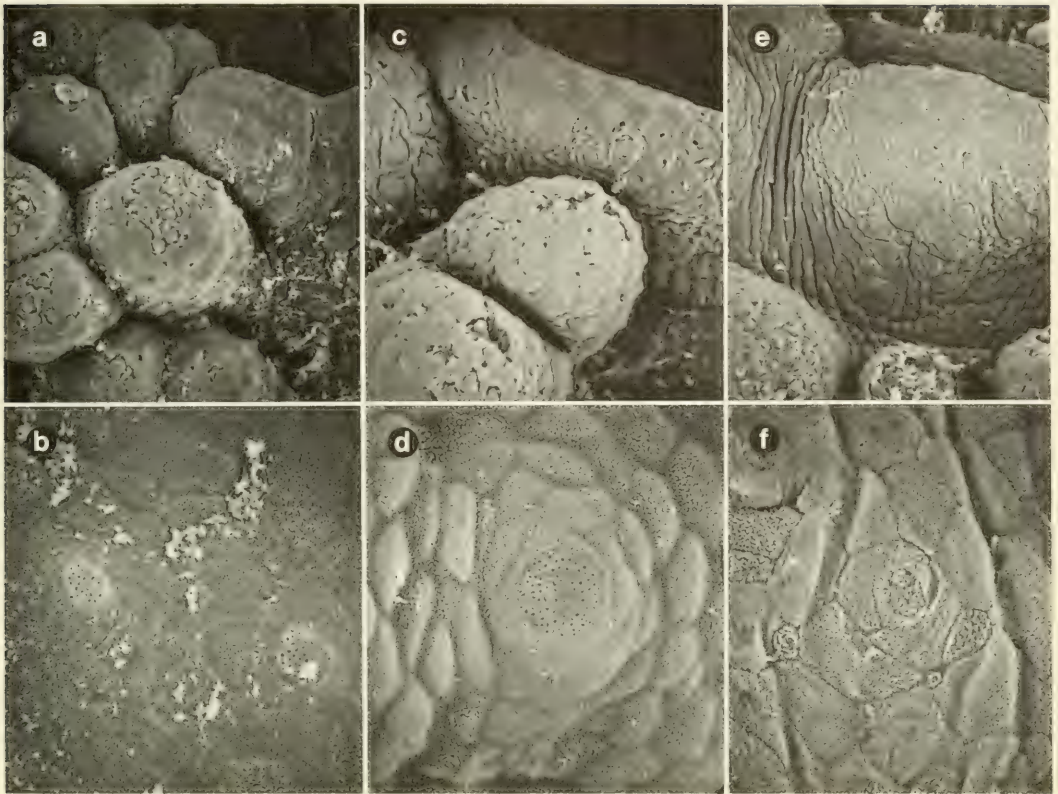


FIGURE 4. Taste buds in Camerounian species of *Chiloglanis* (cont.). a, b, *C. batesii*, 21.7 mm; c, d, *C. disneyi*, 23.0 mm; e, f, *C. niger*, 27.8 mm. Horizontal field widths: a, c, e (top row) = 450 μ m; b, d, f (bottom row) = 45 μ m.

species with greatly reduced barbels and relatively small papillae. *Chiloglanis niger*, with a very large sucker, minute barbels, and moderately large papillae, has taste buds few in number and poorly developed. *Chiloglanis sanagaensis*, with moderately elongate barbels and numerous well-developed papillae, apparently lacks taste buds. Finally, it should be noted that taste buds are not limited to the sucker in *Chiloglanis*. Relatively large buds occur on the dorsal surface of the head in *C. reticulatus* (Fig. 5e, f).

TUBERCLES.—Tubercles, composed of keratinized and sometimes also greatly enlarged superficial epidermal cells, occur on the head and body of all or almost all species of *Chiloglanis*. In contrast to the situation in most cyprinoid fishes, the tuberculation apparently is not sexually dimorphic. Among Camerounian species it is particularly well developed in *C. reticulatus*, *C. polypogon*, and *C. batesii*. Although less evident because they are fewer and further apart, well-de-

veloped tubercles are present also in *C. disneyi*, *C. niger*, and *C. sanagaensis*. The Camerounian (and Zairean) species with the most striking tuberculation is *C. reticulatus*, in which large specimens of both sexes have long tuberculated ridges forming a network or reticulum covering the dorsal and lateral surfaces of the head and much of the body. The ridges are especially evident on the head. They are up to 10 cells wide; the crest of a ridge is regularly tuberculate, each tubercle consisting of about a dozen enlarged epidermal cells (Fig. 5d). The surface of the non-tuberculate polygonal cells forming the ridge is not smooth, the center of each cell being occupied by a low-lying roughened protuberance evidently equivalent to an unculus (for review of unculi see Roberts 1982). The epidermal surfaces between the ridges, in contrast, consist of slightly smaller, non-unculiferous (and therefore relatively smooth-surfaced) polygonal cells, widely scattered taste buds, and even more widely scattered pores. The

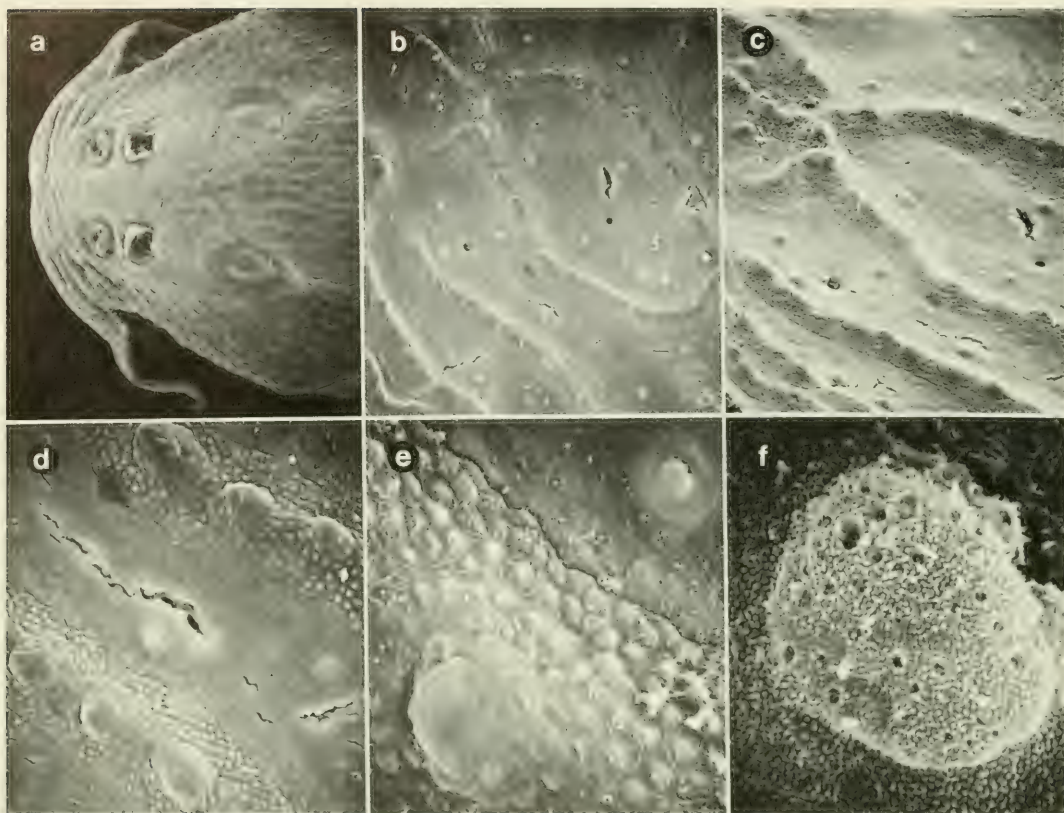


FIGURE 5. Epidermal features on head of *Chiloglanis reticulatus*. *a*, dorsal view of head of 31.3 mm paratype, with elongate tuberculate ridges well developed (but not connecting up to form a network as in larger specimens); *b*–*e*, dorsal surface of head posterior to eye of 41.6 mm holotype, with well-developed network of tuberculated ridges and isolated taste buds; *f*, enlarged view of taste bud in *e*. Horizontal field widths: *a*, 7.5 mm; *b*, 1 mm; *c*, 750 μ m; *d*, 360 μ m; *e*, 110 μ m; and *f*, 11 μ m.

pores, two of which are seen in Figure 5*b, c*, lie in shallow depressions about 50 μ m diameter and are themselves about 20 μ m diameter. The taste buds, elevated above the general epidermal surface, are also about 20 μ m diameter (Fig. 5*f*). The gross aspects of all of these features (but not their cellular nature) can be observed under the dissecting microscope. Although no other species of *Chiloglanis* observed by me has tuberculated ridges forming such an extensive and well-defined network as *C. reticulatus*, more or less elongate tuberculated ridges are present on some larger specimens of *C. batesii*, *C. occidentalis*, and *C. polypogon*.

Numerous round or oval tubercles, comprising some 60 to 80 cells and about 40 μ m diameter, occur on the dorsal surface of the head of *C. polypogon* (Fig. 6*a, b*). Similar tubercles were observed in *C. batesii* from Ngudi (Fig. 6*e*). Some

larger *C. batesii* have tuberculated ridges, but these were not observed with SEM. In *C. polypogon* the cells comprising a tubercle are unicellular, whereas in the specimens of *C. batesii* observed they are not. In a 28.6 mm *C. sanagaensis*, prominent tubercles were observed on the dorsal surface of the snout. These have a round base 30 to 35 μ m diameter, and a rounded or pointed apex to 20 to 30 μ m high. They appear to have a perimetral dehision ring (Fig. 6*d*). The head of this specimen exhibits many shallow crater-like depressions, tentatively identified as scars from tubercles that had been shed. Of the species of *Chiloglanis* examined with SEM, the weakest tuberculation is in *C. niger*. Tubercles on its head are widely separated, up to 40 μ m diameter, but not elevated, consisting of only a single layer of thin, apparently individually dehiscient polygonal epidermal cells, with irregular projections

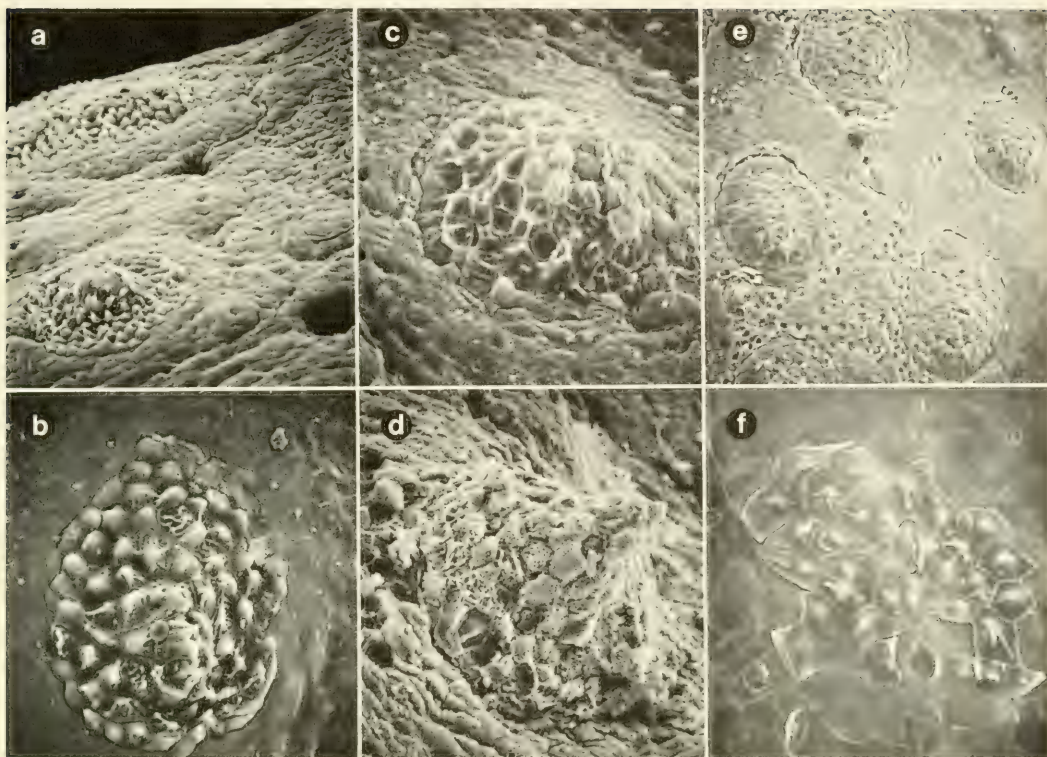


FIGURE 6. Tubercles on head of Camerounian species of *Chiloglanis*. a, b, *C. polypogon*, 25.0 mm; c, d, *C. sanagaensis*, 28.6 mm; e, *C. batesii*, 25.7 mm (R. Ngudi); f, *C. niger*, 27.8 mm. Horizontal field widths: a, 250 μ m; b, c, 115 μ m; d, 105 μ m; e, 450 μ m; and f, 105 μ m.

(unculi?) arising from their centers or cell margins (Fig. 6f).

FIN RAYS.—Counts of fin rays are of limited usefulness in distinguishing species of *Chiloglanis*. Most useful are dorsal and pectoral fin ray counts. Most Camerounian species usually have 5 soft dorsal fin rays, but *C. batesii*, *C. niger*, and *C. voltae* usually have 6. However, occasional specimens of the former species have only 5 and occasional specimens of the latter species have 6. *Chiloglanis harbinger* has 4 or 5. Many species have 7 or 8 soft pectoral fin rays; no species has been observed with fewer than 7. *Chiloglanis disneyi* has 8 or 9, *C. harbinger* and *C. niger* 9 or 10.

In many specimens the number of anal fin rays is difficult to determine. I have not obtained adequate data to evaluate anal fin ray counts for distinguishing species. Camerounian species have a total of 7 to 12 anal fin rays, but much of the variation is in the number of anterior simple

rays, which range from 2 to 5. Especially in specimens with more simple rays, the anteriormost ones tend to be very small, sometimes impossible to count accurately in whole specimens or even in radiographs. The number of branched anal fin rays is usually 7 (range 5 to 8). All species of *Chiloglanis* examined have 7 pelvic fin rays and 8/9 principal caudal fin rays.

COLORATION.—The basic elements of color pattern—lightly and darkly pigmented areas—are remarkably constant in many species of *Chiloglanis*. This can be appreciated readily by comparing the photographs of various Camerounian species in this paper. The main feature of the color pattern is three broad dark vertical bands on the dorsolateral body surface. Although the outline of the bands is irregular, closer examination reveals the same or similar irregularities in the bands of quite different species. This is especially true for the very irregularly shaped second band, lying between the adipose and anal

fins. This band has an anteroventral projection where its ventral portion is more or less extensively broken or invaded by a depigmented area arising between the base of the pelvic and anal fins and extending dorsoposteriorly. The position and shape of this pale area, and the resulting configuration of the dark vertical band between the adipose and anal fins, is very evident in the photos of *C. reticulata*, *C. polypogon*, *C. sanagaensis*, and *C. disneyi*. It is also visible in the photos of *C. niger* and *C. batesii*, although in these specimens the basic pattern is obscured by their overall duskiness. The barred color pattern on the caudal peduncle and caudal fin is similar in many species. Some species, including *C. polypogon* and *C. reticulatus*, have small, round, pale spots scattered on the dark vertical bands of the body. At first glance these spots appear irregular, but their number and position is similar in various species. The peculiar conservatism of the irregularly banded or barred color pattern of *Chiloglanis* is paralleled by a number of other groups of catfishes, notably the Southeast Asian bagrid genus *Leiocassis*.

Most species of *Chiloglanis* are dull and cryptically or disruptively colored in life. Live *Chiloglanis niger* are uniformly dark, almost black. This is perhaps also true in *C. harbinger* for which coloration has been observed only in preserved specimens. The most brilliantly colored species probably is *C. disneyi*, which has well defined bright yellow and black bands. Sexual dichromatism is unknown.

A few species have distinctive color features. Nearly all species have dark vertical bars on the dorsolateral part of the body that end more or less abruptly at about the level of the paired fins. In *C. harbinger* the large anterior bar extends partially onto the abdomen, the melanophores becoming fewer and wider apart towards the ventral midline. In *C. cameronensis* this bar often continues without diminished intensity right across the abdomen, which is therefore black. This is especially so in samples of this species from the Ntem and Ogooue basins. In most specimens of *C. niloticus* and its close relative (or conspecific) *C. occidentalis*, the upper and lower caudal fin lobes each bear a dark horizontal stripe. Although *C. occidentalis* is widely distributed in western Africa, including the Niger basin, it has not been found in Cameroun. None of the species of *Chiloglanis* known from Cameroun have cau-

dal fin lobes with horizontal stripes. The dorsal surface of the snout of *C. batesii* has a triradiate pattern. This consists of a dark or dusky median mark at the snout tip separated by pale interspaces from an anterolateral dark or dusky mark on each side of the snout. This pattern, observed in specimens from throughout the extensive range of *C. batesii*, is absent or poorly developed in other species of *Chiloglanis*. *Chiloglanis reticulatus*, occurring sympatrically with *C. batesii* in the Congo basin, often has a biradiate pattern on the snout. This is due to a dark or dusky anterolateral mark on each side of the snout as in *C. batesii*, but the large intervening area including the snout tip is pale.

SEXUAL DIMORPHISM.—Testes of maturing *Chiloglanis* have numerous lobes. In extremely ripe males the lobes may be so enlarged as to cause abdominal expansion comparable to that of gravid females. In many species males have an elongate genital papilla. Secondary sexual dimorphism occurs in several species. Often this involves enlargement of the anal fin, and sometimes also enlargement and modification of the shape of the caudal fin. In males of *C. macropoterus* Poll and Stewart, 1975, from the R. Luongo in Zambia (Congo basin), the anal and caudal fins are both enlarged; the caudal fin, moderately forked in females, is triangular in large males, with the distal part of the triangle formed by elongation of the middle caudal fin rays. Very similar sexual dimorphism of the anal and caudal fins occurs in a West African species, *C. normani* from the R. Cavally, Cote d'Ivoire. The only Camerounian species in which sexual dimorphism of the caudal fin has been observed is *C. batesii*. In this species the caudal fin is very deeply forked, with the upper lobe considerably enlarged and pointed or even filamentous in mature males. Such modification of the upper caudal fin lobe of male *Chiloglanis* has been reported previously only in *C. micropogon*, here considered conspecific with *C. batesii*. In addition to the enlarged and pointed upper caudal fin lobe, mature males of *C. batesii* have lobate testes, an elongate genital papillae, enlarged anal fin, and one other remarkable feature.

Radiographs of *Chiloglanis* from Cameroun and other countries reveals several species with a striking sexual dimorphism hitherto unreported. In these species males have the humeral process of the pectoral fin girdle more or less

TABLE 2. Vertebral counts in species of the suckermouth mochokid genera *Chiloglanis*, *Atopochilus*, and *Euchilichthys*.

	Abdom- inal	Caudal	Total
<i>C. batesii</i>			
Mungo	15	16-17	31(2), 32(2)
Cross	15	16-17	31(1), 32(1)
Ja	14	17-18	31(3), 32(1)
Luala	14-15	16-17	30(2), 31(7)
Lufu	14-15	15-17	30(4), 31(5), 32(1)
Inkisi	14-15	16-17	31(5), 32(5)
Kwango	15-16	16	31(1), 32(5)
Mbomou	14-15	16-17	31(2)
Kivu	15	17-18	32(1), 33(1)
<i>C. brevibarbis</i>			
Athi	15-17	18-20	34(3), 35(10)
<i>C. camerounensis</i>			
Lokunje	15	15-16	30(1), 31(1)
Mvila	14-15	16-17	31(4)
Ntem	15	16	31(2)
Diala	15	16-17	31(2), 32(1)
Ivindo	14-15	16	30(2), 31(2)
<i>C. congicus</i>			
Congo	16-17	15-16	32(3), 33(1)
<i>C. deckenii</i>			
Kerio	16-18	15-17	33(4), 34(2)
<i>C. disneyi</i>			
Mungo	15	15-16	30(1), 31(1)
Cross	15-16	15-17	31(6), 32(3)
<i>C. harbinger</i>			
Lokunje	15-16	15-16	30(1), 31(9)
<i>C. niger</i>			
Menchum	15	16	31(1)
<i>C. occidentalis</i>			
Ankwao	14-15	16-18	31(1), 32(3)
Pra	14-15	16-18	31(4), 32(2)
<i>C. polyodon</i>			
Bagbwe	15	16	31(1)
<i>C. polypogon</i>			
Cross	14-15	16-18	30(1), 32(10), 32(8)
<i>C. reticulatus</i>			
Congo	14-15	16-19	31(5), 32(4), 33(5)
<i>C. sanagaensis</i>			
Sanaga	14-16	16-17	31(1), 32(4), 33(1)
<i>C. sardinhai</i>			
Caimbambo	14-15	15-17	30(1), 31(4)
<i>C. voltae</i>			
Oti	13-14	16-17	29(2), 30(5), 31(2)
Lakdo	13-14	16-18	30(3), 31(1)
<i>A. savorgnani</i>			
Ntem	17-18	14-15	32(5), 33(3)

TABLE 2. Continued.

	Abdom- inal	Caudal	Total
<i>A. sp. undet. a</i>			
Stanley Pool	19	16	35(1)
<i>A. sp. undet. b</i>			
Lufu	21	16	37(1)
<i>E. dybowskii</i>			
Oubanghi	19	13	32(1)
Mbomou	18-20	12-14	31(2), 32(2)
<i>E. royauxi</i>			
Kinsuka	23-24	17-18	40(1), 42(1)

greatly enlarged. The enlargement is manifested externally as a large, skin-covered convex boss just above the pectoral fin. It is most pronounced in *C. batesii*, but also occurs in *C. occidentalis* and *C. polypogon*. It apparently does not occur in *C. brevibarbis*, *C. camerounensis*, *C. congicus*, *C. disneyi*, *C. niger*, *C. reticulatus*, *C. sanagaensis*, or *C. voltae*, for all of which radiographs as well as specimens have been examined.

VERTEBRAL COUNTS.—Vertebral counts, until recently seldom employed in systematic studies of catfishes, can be very useful in distinguishing species. Smaller or less elongate species of catfishes often have fewer vertebrae than their larger or more elongate close relatives. Thus, the sisorid catfish *Bagarius bagarius* Hamilton-Buchanan, 1822, is a small species superficially similar to the very large species *Bagarius yarrelli* Sykes, 1841, but differs from it in having only 38-42 (mode 39) vertebrae instead of 40-45 (mode 43) (Roberts 1983:437). Vertebral counts are of comparable utility in distinguishing species of the bagrid genera *Leiocassis* and *Mystus* and of the pangasiid or schilbeid genus *Pangasius* (Roberts, in press). Vertebral counts are determined readily from radiographs of *Chiloglanis*. In some catfish groups, due to variation in the length and partial or total fusion of the anteriormost (Weberian) vertebral centra with each other, and occasional fusion of additional more-posterior vertebrae with them, it is difficult to obtain reliable counts of abdominal vertebrae. In *Chiloglanis*, however, the four Weberian vertebrae have centra of about the same size that remain separate; thus, they often may be counted directly from radiographs. Furthermore, the fourth vertebra is

readily identifiable by the large ossa suspensoria and the fifth vertebra by a large but slender pair of normally shaped ribs. In practice I commence a count of the vertebral column with the fifth vertebra and proceed backwards. Abdominal vertebrae are defined as all those lying anterior to the anal fin and its pterygiophores. If the anteriormost anal fin pterygiophore approximates or even contacts the hemal spine of a vertebra but fails to lie in front of it, the vertebra is counted as abdominal. The hypural complex is counted as one vertebra. This method gives repeatable counts for most catfishes and many other fish groups. Vertebral counts from a radiographic survey of *Chiloglanis* and other mochokid genera with sucker mouths are presented in Table 2.

The counts are of little use in distinguishing most species of *Chiloglanis*, all of which are more or less short bodied and none very large. Many species have around 30 or 31 to 33 vertebrae. The smallest species, *C. voltae*, has 29–31. This is close to the lowest number of vertebrae found in other groups of catfishes and in ostariophysan fishes generally. Somewhat higher counts (33–35) occur in species from East Africa including *C. deckenii* and *C. brevibarbis*. Of particular interest are the vertebral counts of the genera *Atopochilus* and *Euchilichthys*, in which the species generally are far larger (to 600 mm) than *Chiloglanis* and have up to 42 vertebrae. In addition there is a shift in the ratio of abdominal to caudal vertebrae. In *Chiloglanis* the ratio is close to unity, $n:n$ or $n:n+1$ or $n+2$, while in *Atopochilus* and *Euchilichthys* the abdominal vertebrae are more numerous than the caudal vertebrae, so the ratio is $n:n-2$ to $n-7$. This increase in abdominal vertebrae appears related to an elongate abdomen accommodating an extremely convoluted gut.

SYSTEMATIC ACCOUNT

Chiloglanis Peters, 1868

***Chiloglanis* Peters, 1868:** 599 (type species *Chiloglanis deckenii* Peters, 1868, by monotypy).

Chiloglanis (gender masculine) differs from all other genera of the endemic African catfish family Mochokidae, except *Atopochilus* Sauvage, 1878 and *Euchilichthys* Boulenger, 1900, in having upper and lower lips greatly expanded and united to form a sucker. Some species of *Synodontis* have large lips superficially resembling

those of *Chiloglanis* but are readily distinguishable because they have mental barbels free from sucker instead of incorporated into it. In *Atopochilus* and *Euchilichthys* the mandibular teeth are very numerous and spread across the entire free margin of the lower jaw, whereas in all species of *Chiloglanis* except *C. voltae*, the mandibular teeth are relatively few and restricted to a relatively small area near the symphysis of the lower jaw. In *Chiloglanis* the pectoral fin spine is invariably smooth, never serrate, while in *Atopochilus* and *Euchilichthys* it bears few to many serrae. *Euchilichthys* and *Atopochilus* are very poorly represented in Cameroun. *Euchilichthys dybowskii* is present in the R. Ngoko (lower R. Ja, Congo basin) and *Atopochilus savognani* in the R. Ntem.

KEY TO *CHILOGLANIS* OF CAMEROUN

- 1A. Mental barbels moderately to very long (Fig. 1a–c) 2
- 1B. Mental barbels short, sometimes absent (Fig. 1d–f) 7
- 2A. No auxiliary mental barbels (Fig. 1a) 3
- 2B. From 2 to 5 well developed auxiliary mental barbels on each side of lower lip (Fig. 1b) 4
- 3A. Sucker with well developed papillae; large teeth on premaxilla in several rows; mandibular teeth well developed; adults to over 40 mm (Congo basin) ... *C. reticulatus*
- 3B. Sucker without papillae; large teeth on premaxilla in two rows; mandibular teeth in two rows; adults to 27 mm (Niger basin) *C. voltae*
- 4A. Mental barbels very large; sucker transversely oval, middle of lower lip with greatly enlarged papillae (Fig. 1a, b) 5
- 4B. Mental barbels moderately large; sucker round, or longer than broad, entire surface covered with papillae of similar size (Fig. 1c) 6
- 5A. Accessory mental barbels no more than 3 on each side of lower lip; mandibular teeth 4+4 to 7+7 (Niger basin) *C. benuensis*
- 5B. Accessory mental barbels from 3 to 5 on each side of lower lip; mandibular teeth 3+3 or 4+4 (Cross basin) *C. polypogon*
- 6A. Body relatively elongate; abdomen not greatly expanded, more or less extensively darkly pigmented; mandibular teeth

- 4+4 to 8+8 (coastal basins east of Sanaga basin) *C. cameronensis*
- 6B. Body stubby; abdomen considerably expanded, pale; mandibular teeth usually 4+4 or 5+5, rarely 6+6 (Sanaga basin) *C. sanagaensis*
- 7A. Mandibular teeth (except in very small specimens) 8+8 or more; sexual dimorphism absent or weak 8
- 7B. Mandibular teeth 3+3 to 6+6; sexual dimorphism marked, larger males with enlarged anal fin, enlarged and pointed upper lobe of caudal fin, and greatly enlarged and expanded humeral process of pectoral girdle (in all or nearly all river basins) *C. batesii*
- 8A. Sucker relatively huge; large premaxillary teeth in seven or eight rows; top and sides of body extensively covered with melanophores, so it appears almost uniformly dark; pectoral fin soft rays 9 or 10; caudal peduncle moderately to very slender 9
- 8B. Sucker relatively small; large premaxillary teeth in three or four rows; top and sides of body with very sharply contrasting dark vertical bands alternating with pale areas; pectoral fin soft rays 8 or 9; caudal peduncle relatively deep *C. disneyi*
- 9A. Mandibular teeth 8+8 to 10+10; dorsal fin soft rays 6; adipose fin short (Niger basin) *C. niger*
- 9B. Mandibular teeth 13+13 to 15+15; dorsal fin soft rays 4 or 5; adipose fin long (Lokunje basin) *C. harbinger*

Chiloglanis reticulatus new species

(Figs. 1a, 2, 3a, b, 5, 7)

HOLOTYPE.—CAS 60786, 41.6 mm gravid female, Cameroun, Congo basin, R. Mwamedjwel, a very small stream 2–3 km W of Yokadouma, Tyson R. Roberts, 15 Jan. 1980.

PARATYPES.—CAS (SU) 47471, 36.3 mm, Cameroun, Congo basin, R. Momjepom, Yokadouma, A. I. Good, 20 Mar. 1936; CAS 60787, 31.0 mm, Zaire, Congo basin, R. Lubazi, tributary of R. Lua, 3 km S of Kibunzi, Tyson R. Roberts and Donald J. Stewart, 17 Aug. 1973; CAS 60788, 10: 19.1–38.1 mm, Zaire, Congo basin, R. Lufu, 2 km NW of Lufu village, Tyson R. Roberts and Donald J. Stewart, 2 Aug. 1973 CAS 60789, 43: 9.4–37.4 mm, Zaire, Congo basin, tributary of R. Lua 26 km N of Kibunzi, Tyson R. Roberts and Donald J. Stewart, 17 and 24 Aug. 1973.

Chiloglanis reticulatus is a relatively small species, largest specimen 41.6 mm standard length; sucker relatively small, transversely oval,

with very large barbels; auxiliary mental barbels absent; large teeth of premaxillary in 2 to 4 rows; mandibular teeth in 1 or 2 rows, very irregularly arranged, basic count from about 2+2 to 5+5; eyes large; dorsal fin soft rays usually 5 (rarely 6); pectoral fin soft rays 7 or 8; adipose fin long, its origin well in advance of a vertical line through anal fin origin; caudal peduncle moderately deep; caudal fin moderately forked, lower lobe longer than upper. Larger specimens of both sexes with well-developed tuberculated epidermal ridges on head and body, characteristically forming a dense network or reticulum on dorsal surface of head. The largest male, 37.4 mm, from tributary of R. Lua, has anal fin and lower lobe of caudal fin greatly enlarged; humeral process of pectoral spine not enlarged. Its genital papilla is elongate, with a peculiarly enlarged and swollen tip, so that it resembles somewhat the proboscis of an elephant. Sexual dimorphism absent or slight in other specimens examined. Holotype in life with chocolate-brown dark bands and cream-colored interspaces.

ETYMOLOGY.—The name *reticulatus* (Latin, adjective) refers to the reticulum or network of tuberculated epidermal ridges.

DISTRIBUTION.—Known only from the north-western portion of the Congo basin in Cameroun and Zaire.

Chiloglanis voltae Daget and Stauch, 1963

Chiloglanis voltae Daget and Stauch, 1963:99, fig. 4 (type locality Bougouri Ba au pont de Nabéré, Volta basin; also reported from R. Benoué à Lakdo, Cameroun); Roman 1966: 154 (Volta Noire près de Boromo).

MATERIAL EXAMINED.—CAMEROUN: **Niger basin:** MNHN 1962-1275, 53: 14.6–17.6 mm, R. Benoué à Lakdo (paratypes); **NIGERIA: Niger basin:** CAS 64128, 33: 16.9–27.0 mm, R. Benue 22 km E of Makurdi; **GHANA: Volta basin:** MNHN 1984-551, 102: 15.1–26.3 mm, R. Oti à Sabari; MNHN 1984-522, 2: 22.9–27.2 mm, R. Wawa à Yadzo. **BURKINA FASO: Volta basin:** MNHN 1962-1280, 24.2 mm, Bougouri Ba au pont de Nabéré (holotype); MNHN 1961-591, 24: 14.6–16.9 mm, same collection as holotype (paratypes).

Chiloglanis voltae is the smallest known species of *Chiloglanis*, largest specimen 27.2 mm standard length. Sucker moderately large, non-papillose; outer mental barbel elongate, inner short; no auxiliary mental barbels; teeth conical, not strongly S-shaped; mandibular teeth in 1 or 2 irregular rows, not concentrated near symphysis but spread across entire mouth opening; eye large; dorsal fin soft rays usually 6; pectoral fin soft rays



FIGURE 7. *Chiloglanis reticulatus*, holotype, gravid female 41.6 mm (Congo basin).

7 or 8; caudal peduncle moderately deep; caudal fin moderately forked; caudal fin lobes rounded, lower slightly longer than upper. Body with three dark or dusky vertical bars separated by pale areas; margin of dark bars defined by concentration of melanophores not observed in other species of *Chiloglanis*; caudal fin without well developed bars or other marks. Sexual dimor-

phism unknown. No observations available on gonads of mature individuals. Total vertebrae 29–31, fewer than in any other species of *Chiloglanis* for which data are available.

DISTRIBUTION.—Known only from the R. Benue (Niger basin) of Cameroun and Nigeria and the Volta basin. In the R. Benue near Makurdi, I collected *C. voltae* on sandy bottom, far from

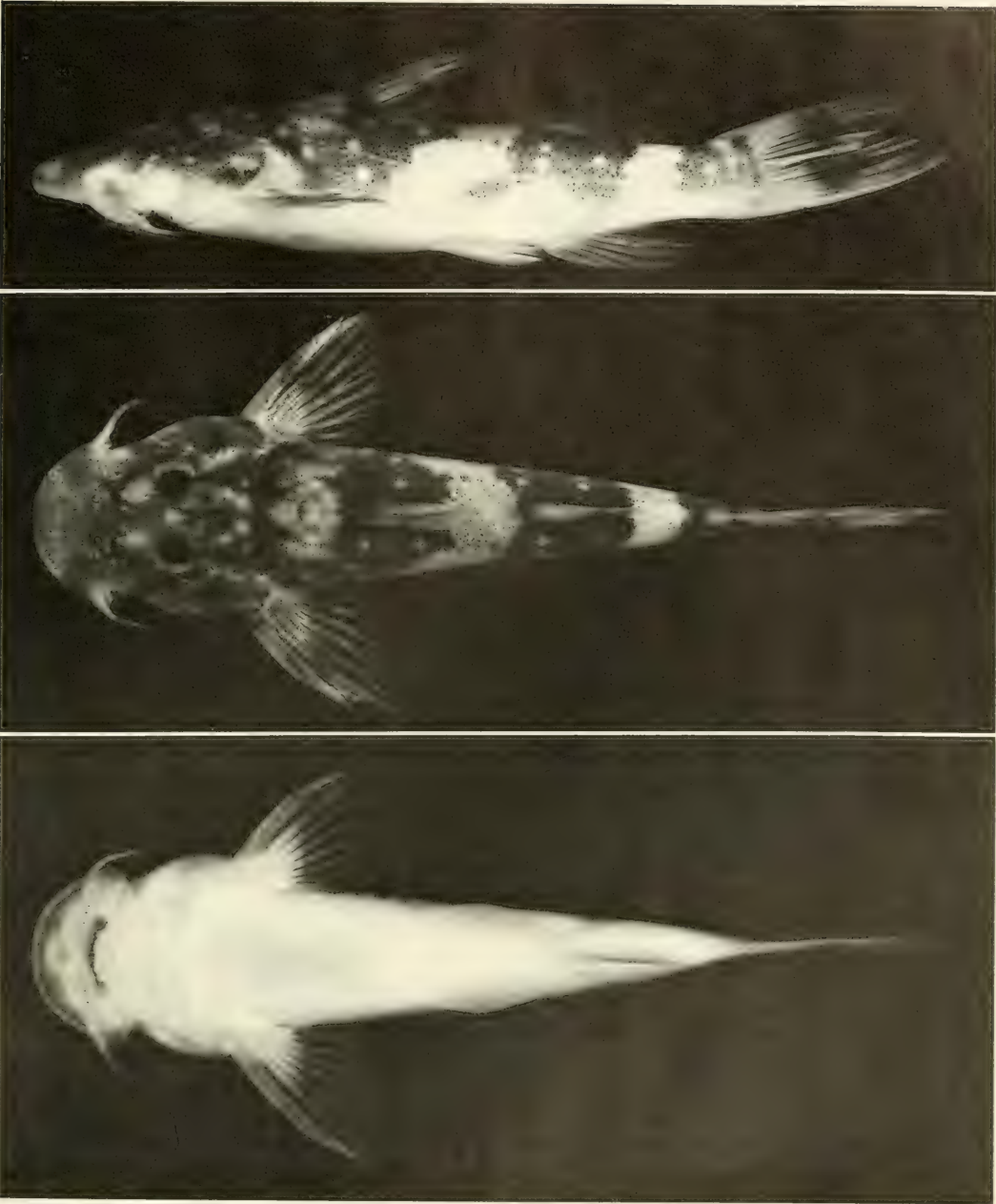


FIGURE 8. *Chiloglanis polypogon*, holotype, immature female 41.5 mm (Cross basin).

any other kind of habitat, in sympatry with *C. benuensis*.

***Chiloglanis benuensis* Daget and Stauch, 1963**

Chiloglanis benuensis Daget and Stauch, 1963:98, fig. 3 (type locality R. Benoué à Lakdo, Cameroun).

MATERIAL EXAMINED.—CAMEROUN: Niger basin: MNHN 1962-1273, 38.4 mm, R. Benoué à Lakdo (holotype); MNHN 1962-1274, 40: 18.9–34.8 mm, collected with holotype (paratypes); NIGERIA: Niger basin: CAS 64127, 20: 20.3–35.0 mm, R. Benue 22 km E of Makurdi.

Chiloglanis benuensis (largest specimen 38.4 mm) has relatively small, transversely oval suck-

er and very large barbels; up to three auxiliary mental barbels on each side of lower lip, but no auxiliary barbel lying external to outer primary mental barbel; eye large; mandibular teeth 3+3 to 5+5; soft dorsal fin rays 5 or 6; pectoral fin soft rays 8; adipose fin long, its origin far anterior to a vertical line through anal fin origin; caudal peduncle moderately slender; caudal fin moderately forked, lower lobe somewhat longer than upper; sexual dimorphism unknown.

DISTRIBUTION.—*Chiloglanis benuensis* is known only from the R. Benue in Cameroun and Nigeria. In the Benue near Makurdi it was collected sympatrically with *C. voltae* on a sandy bottom in shallow, swift-flowing water.

***Chiloglanis polypogon* new species**

(Figs. 1b, 2b, 3c, d, 6a, b, 8)

HOLOTYPE.—CAS 60790, 41.5 mm immature female, Cameroun, Cross basin, high gradient streams along road from Mamfe to Bamenda, 88–94 km SW of Bamenda, Tyson R. Roberts, 17 Mar. 1980.

PARATYPES.—CAS 60791, 11: 20.2–39.7 mm, collected with holotype; CAS 60792, 11: 23.0–26.0 mm, Cameroun, Cross basin, riffles of R. Badi where it flows into R. Cross and main-stream of R. Cross near Mamfe, Tyson R. Roberts, 1–5 Mar. 1980; CAS 60793, 7: 46.4–54.9 mm, Cameroun, Cross basin, small stream on road from Mamfe to Bamenda, 98 km from Bamenda and about 24 km from Mamfe, Tyson R. Roberts, 17 Mar. 1980; MRAC 76-32-P-2213-218, 3: 35.4–38.9 mm, Cross basin, 14 miles [23 km] W of Mamfe towards Eyomojok, H. Stenholt Clausen and Jorgen J. Scheel, 8 Mar. 1966.

Chiloglanis polypogon is a moderately large species, largest specimen 54.9 mm; sucker relatively small, transversely oval, with large papillae and very large barbels; 3–5 auxiliary mental barbels present on each side of lower lip; majority of specimens with an auxiliary mental barbel external to outer primary mental barbel on one or both sides of lower lip (not observed in any other species of *Chiloglanis*); large premaxillary teeth in 3 or 4 irregular rows; mandibular teeth large, 3+3 or 4+4; dorsal fin soft rays usually 5 (5 in 24 specimens, 6 in 5); pectoral fin soft rays 7 or 8; adipose fin long, its origin well in advance of a vertical through anal fin origin; caudal peduncle moderately slender; caudal fin moderately forked, lower lobe longer than upper; larger specimens with longitudinally oriented tuberculated epidermal ridges on dorsal surface of head; sexual dimorphism absent or slight, males without enlarged humeral process. In life pale areas between dark vertical bars and entire ventral surface pinkish or pale salmon,

unlike any other species observed by me. Bars on body intermediate in distinctness between those of *C. disneyi* (very distinct) and *C. batesii* (poorly defined), species with which it occurs sympatrically in Cross basin. Body with pale round spots observed in *C. reticulatus* and some other species but not in *C. batesii* and *C. cameronensis*.

Pupil of eye with flattened upper margin, contractile; contraction involves downward progression of a silvery membrane or “curtain” from ventral margin of exposed portion of eyeball. During maximum contraction, pupil is dorsally directed, almost out of horizontal line of vision. A contractile pupil has not been observed in other species of *Chiloglanis*.

ETYMOLOGY.—The name *polypogon* (noun in apposition, from the Greek “poly,” multiple, and “pogon,” beard) refers to the numerous mental barbels.

DISTRIBUTION.—Known only from the Camerounian portion of the Cross basin.

***Chiloglanis cameronensis* Boulenger, 1904**

Chiloglanis cameronensis Boulenger 1904:18 (type locality Efulen, S. Cameroon); Boulenger 1911:482, fig. 360; Matthes 1964:118 (R. Kululu, tributary of R. Tshuapa near Ikela, Cuvette Centrale of Congo basin, Zaïre; identification doubtful, specimen unavailable for examination); Géry 1965:379 (swamps of R. Ivindo near Makokou, Ogooué basin, Gabon; Roman 1971:134, fig. 58 (Ntem basin, Río Muni).

MATERIAL EXAMINED.—CAMEROUN: BMNH 1904.7.1:90–96, 7: 32.5–41.2 mm, Efulen, Bates collection (syntypes); BMNH 1906.5.28:68–69, 45.3 mm, Efulen (Bates collection); CAS(SU) 15448, 42.0 mm, Efulen, R. Chenge, Kribi basin; CAS(SU) 47468, 25.5 mm, R. Mfiande or R. Seng, Ebolowa, Ntem or Campo basin; CAS(SU) 15450, 36.3 mm, R. Mfiande, Ebolowa, Ntem basin; CAS(SU) 15451, 4: 35.7–40.2 mm, “Ebolowa (Mejap II 12 mi W) Minya’a R. trib. of Mvila R.”; CAS(SU) 47470, 2: 25.6–34.2 mm, Bikui, Lolodorf, Lokunje basin; MHNG 757.69, 33.3 mm, Efulen; MNHN 1988-1163, 3: 34.3–42.9 mm, R. Tchengué on road from Kribi to Ebolowa, about 80 km W of Ebolowa, Kienke basin. RIO MUNI: MRAC 173147–148, 28.7 mm, R. Guoro, tributary of R. Ntem. GABON: MRAC 73-02-P-1911-921, 5: 23.5–33.7 mm, Ogooué basin, Makoukou; MHNG 2169.56–58, 4: 18.9–26.5 mm, Ogooué basin, marigots après Ybiegn, Makoukou; MRAC 80-27-P-89-95, 4: 19.6–28.2 mm, R. Diala.

Chiloglanis cameronensis is a medium-sized species, largest specimen 45.3 mm; sucker very large, longer than broad (not transversely oval), extensively covered with moderately large papillae; barbels short, but well developed, usually papillose; up to 3 auxiliary mental barbels on each side of lower lip; large premaxillary teeth

in 3 or 4 rows; mandibular teeth large, usually about 4+4 or 5+5, but some specimens with as many as 7+7 or 8+8; eyes large; dorsal fin soft rays usually 5; pectoral fin soft rays 7 or 8; adipose fin long, its origin considerably in advance of a vertical through anal fin origin; caudal peduncle moderately to very slender (most slender in specimens from Ogooué); caudal fin not deeply forked, lobes rounded or even truncate, lower slightly longer than upper. Dark bands and pale interspaces on body fairly distinct. Abdomen more or less darkly pigmented, almost black in some specimens, due to melanophores continuous with those on anterior vertical bar of body extending across abdomen. This abdominal pigmentation, absent or poorly developed in other species, highly variable: in some older and poorly preserved specimens, scarcely evident; in some specimens from Cameroun (including Efulen), on only a relatively small area between the pelvic fin bases; in specimens from Ntem and Ogooué, entire abdomen darkened.

DISTRIBUTION.—Coastal basins of SE Cameroun and Rio Muni, including Lokunje, Kribi, Kienke, and Ntem basins; Ogooué basin (Gabon). Only species of *Chiloglanis* known from Ogooué.

Chiloglanis sanagaensis new species

(Figs. 1c, 2c, 3e, f, 6c, d, 9)

HOLOTYPE.—CAS 60794, 26.8 mm male, Cameroun, Sanaga basin, gravel bars and riffles in lower 1–2 km of R. Nchit where it flows into R. Mbam (site of summer palace of Sultan of Fomuban), Tyson R. Roberts, 23 Mar. 1980.

PARATYPES.—CAMEROUN: CAS 60795, 25: 18.6–28.6 mm, collected with holotype; MNHN 1988-1164, 11: 31.4–39.9 mm, Sanaga basin, R. Makénéné at bridge on road to Ndimeki (100 m from Bafia-Bafoussam route), about 110 km S of Bafoussam, Tyson R. Roberts, 1 Jan. 1988; MNHN 1988-1165, 12: 21.1–42.8 mm, Sanaga basin, R. Mana 23 km N of Bafia on route from Bafia to Bafoussam, Tyson R. Roberts, 1 Jan. 1988.

Chiloglanis sanagaensis is a medium-sized species, largest specimen 42.8 mm; sucker moderately large, round, with numerous papillae of uniform size evenly distributed over almost its entire surface; barbels short but well developed, each side of lower lip with 3 auxiliary mental barbels; large premaxillary teeth in 3 or 4 rows; mandibular teeth usually 4+4 or 5+5, rarely 6+6; eyes moderately large; dorsal fin soft rays 5 or 6; pectoral fin soft rays 7 or 8; adipose fin low and very long, its origin far in advance of a vertical through anal fin origin; caudal peduncle

slender; caudal fin almost truncate, very slightly emarginate or forked, lobes slightly rounded, lower a bit longer than upper. Secondary sexual dimorphism not observed.

This species characterized by short, stocky or stubby body and swollen abdomen. Swelling evident in virtually all specimens, seemingly due mainly to exceptionally long and highly coiled intestine. A specimen of 27.0 mm has intestine just over 30 mm long, more than double relative length of intestine observed in *C. batesii* and several other species.

ETYMOLOGY.—The name *sanagaensis*, adjective, refers to the Sanaga basin, source of all known specimens of this species.

DISTRIBUTION.—Known only from the Sanaga basin.

Chiloglanis batesii Boulenger, 1904

(Figs. 1d, 2d, 4a, b, 6e, 10)

Chiloglanis batesii Boulenger, 1904:19 (type locality “Efulen” and “streams tributary of the Lobi River, 15 or 20 miles S.W. of Efulen” [South Cameroon]); Boulenger 1911:485, fig. 363 (Efulen, R. Lobi, R. Ja); Nichols and Griscom 1917: 720 (lower Congo; Faradjé; no description); Trewavas 1974 (morphology, comparison with *C. micropogon*).

Chiloglanis micropogon Poll, 1952:228, figs. 3, 4 (type locality R. Nzokwe, affluent de la R. Ulindi, Territ. Kabare; and R. Tshinganda, Bunyakiri, affluent de la R. Luhoho, West Kivu); Daget 1954:307, fig. 116 (upper Niger); Poll 1967:255, fig. 119 (R. Luachimo, Angola); Trewavas 1974:361, figs. 5, 6 (Mungo, Meme, and Lobi basins, Cameroun; R. Kaduna, Niger basin, Nigeria).

MATERIAL EXAMINED.—CAMEROUN: BMNH 1904.7.127, 28.2 mm, “15 or 20 miles S.W. of Efulen in streams trib. to R. Lobi” (syntype, a male with elongate genital papilla, elongate upper caudal fin lobe, and enormously expanded humeral process); BMNH 1904.7.1.97–100, 4: 27.8–33.2 mm, Efulen, Bates collection (syntypes); BMNH 1904.10.26:53–62, 11: 27.5–34.0 mm, R. Ja; BMNH 1909.4.29.97, 26.1 mm, R. Lobi; CAS 60796, 2: 36.7–39.3 mm, high-gradient streams along Mamfe-Bamenda road, 16–22 km N of Numba and 88–94 km SW of Bamenda. Cross basin; CAS 60797, 22.2 mm, riffles in mouth of R. Badi where it flows into R. Cross at Mamfe; CAS 60798, 6: 19.2–26.7 mm, R. Nchit where it flows into R. Mbam, Sanaga basin; BMNH 1973.5.14:362–363, 2: 19.8–20.0 mm, R. Mungo at Baduma; BMNH 1973.5.14:347–354, 3: 13.7–24.5 mm, R. Blackwater, Mungo basin; BMNH 1973.5.14: 355–359, 2: 22.0–26.3 mm, R. Dilolo at Bolo, Mungo basin; BMNH 1973.5.14:364–370, 2: 31.9–35.8 mm, R. Wowe, Mungo basin; CAS(SU) 15447, 9: 29.0–33.3 mm, Efulen, R. Chenge, Kribi basin; MNHN 1988-1155, 3: 26.2–28.7 mm, Kienke basin, R. Tchengué on road from Kribi to Ebolowa. GUINEA: Niger basin: MNHN 1986-750, 85: 18.5–34.6 mm, R. Milo. MALE: Niger basin: MNHN 1961-590, 14: 30.1–35.2 mm, Oeyanko, near Bamako. NIGERIA: Niger basin: MNHN 1988-1154, 4: 21.7–37.8 mm, R. Owena 25 km NE of Ondo on road to

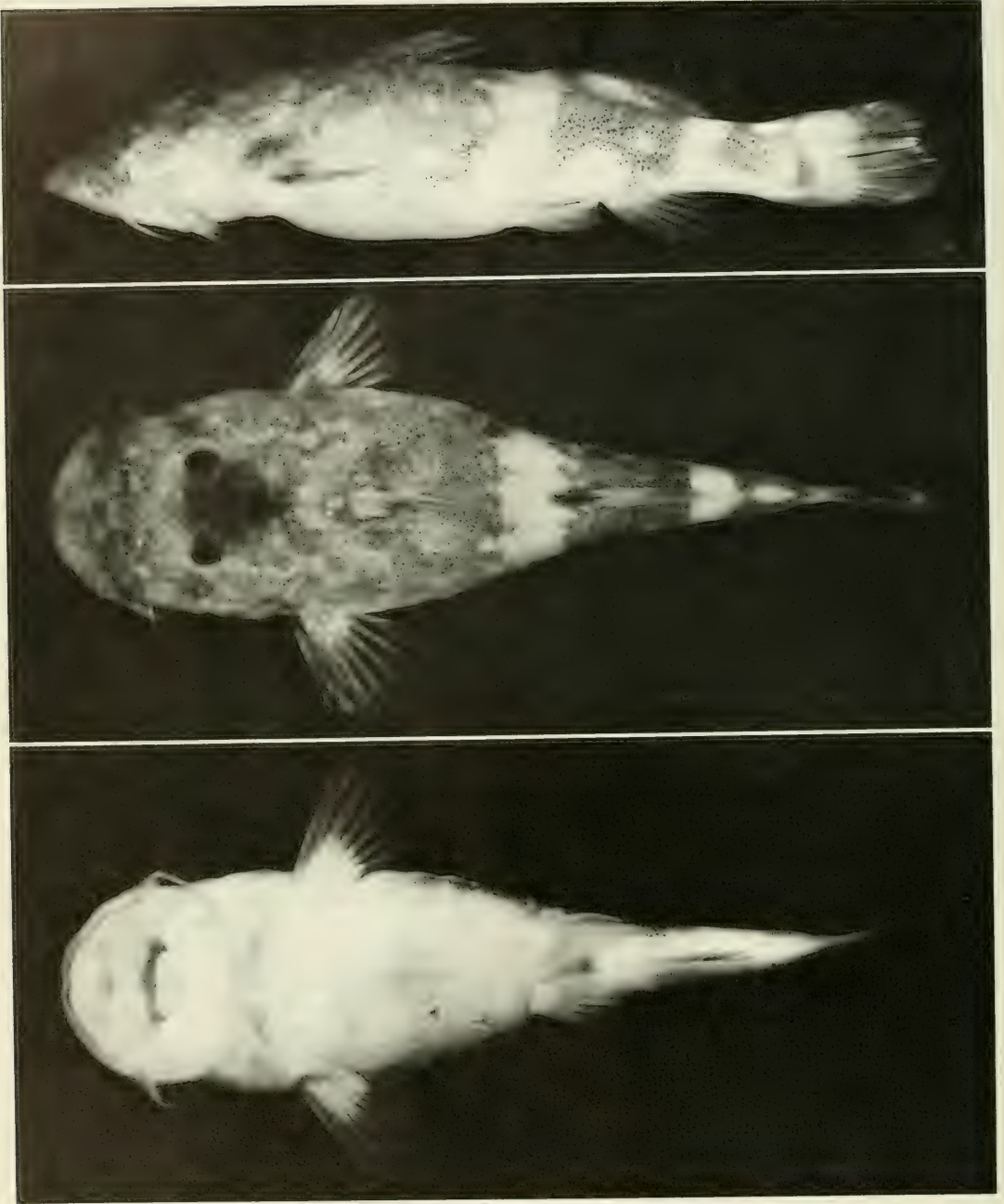


FIGURE 9. *Chiloglanis sanagaensis*, holotype, male 26.8 mm (Sanaga basin).

Akure: MNHN 1988-1153, 8: 16.3–20.0 mm, R. Osse near Uyere, on road from Benin City to Akure; BMNH 1978.12.13.7–8, 2: 26.5–27.3 mm, Gurara Falls near Abuja; MNHN 1977-14, 3: 24.1–37.6 mm, R. Lere, Gindiri, Jos Plateau; MNHN 1977-15, 3: 27.1–40.0 mm, R. Shemankar, tributary of R. Gu, Jos Plateau; Victor. G. Smith collection, uncat., 34.9 mm, R. Assob, Gengera Kibo, Jos Plateau. REPUBLIQUE CENTRAFRI-

CAINE: Chad basin: MNHN 1988-1156, 8: 21.5–27.5 mm, R. Doukouma about 65 km W of Mbres; MNHN 1988-1157, 131: 19.3–31.8 mm, R. Ouaham 20 km upriver from Batangafo; MNHN 1988-1158, 2: 31.3–36.1 mm, R. Koumbala below Chutes de Matakil; MNHN 1988-1159, 5: 22.2–25.7 mm, R. Gounda (near Chad border). Congo basin: MNHN 1988-1161, 20: 18.2–31.6 mm, R. Mbomou near Zemio; MCZ 48360,

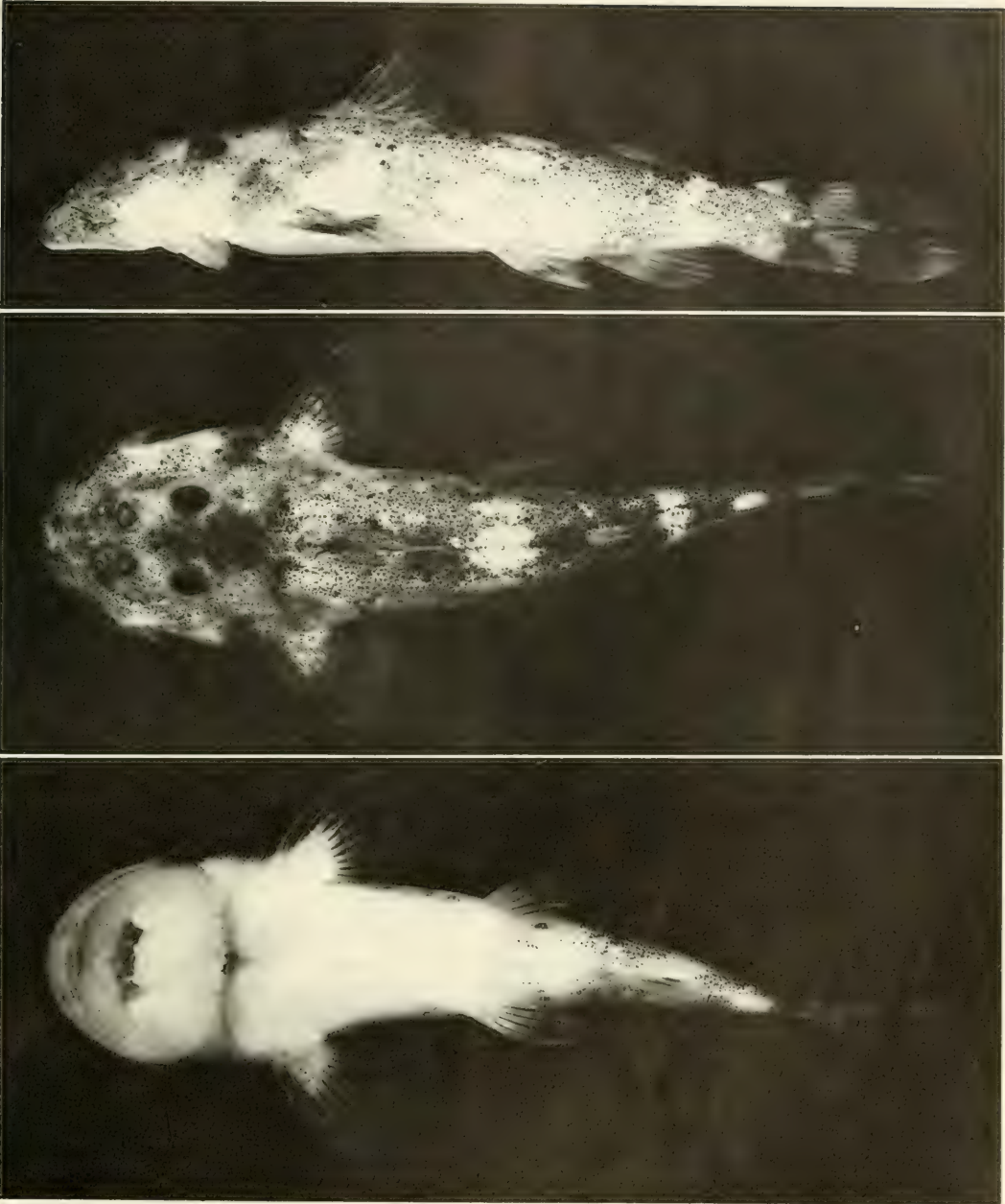


FIGURE 10. *Chiloglanis batesii*, 36.7 mm (Sanaga basin).

R. Mbomou at rapides de Gozobangui; MNHN 1988-1160, 41: 17.6–29.6 mm, R. Chinko at Rafai; MNHN 1988-1162, 4: 31.3–36.0 mm, small tributary of R. Euwou about 30 km NW of Alindao. **ZAIRE: Congo basin:** CAS 60799, 26.4 mm, R. Yambi below Chute de Bidi, 21 km E of Sundi-Mamba; CAS 60800, 60: 16.5–27.2 mm, R. Ngudi at Chute Mayeux, 23 km NE of Sundi-Lutete; CAS 60801, 139: 13.7–30.4 mm, R. Lufu, Songoloko district; CAS 60802, 2: 22.7–25.7 mm, R. Lubazi, tributary to R. Lua near Kibunzi; CAS 60803, 35: 19.2–29.3 mm, tributary to R. Lua near Kibunzi; CAS 60804, 25.8 mm, R. Kwilu near Moerbeke; 60805, 29.6 mm, R. Sengezi, tributary to R. Inkisi-Lukusu 87 km W of Kinshasa; CAS 60807, 2: 23.9–26.4 mm, R. Konzi, tributary to R. Kwango, at bridge on road from Kenge to Masi-Manimba; FMNH 62918, 22.2 mm, R. Dungu, Nagero; MRAC 91480-81, 2: 33.1–37.2 mm, R. Tshinganda, tributary of R. Luhoho, Bun-

yakiri, Kivu (paratypes of *C. micropogon*); MNHN 1987-1607, 32.0 mm, R. Loya near Mafifi.

Chiloglanis batesii is a small species, largest known specimen 40 mm standard length; sucker relatively large, round or longer than broad rather than transversely oval; mental barbels greatly reduced; mandibular teeth 6+6 or fewer (often 5+5, occasionally 4+4); eyes large; dorsal fin soft rays usually 6 (sometimes 5); pectoral soft rays 7 or 8; adipose fin high and posteriorly rounded, but relatively short, its origin only slightly in advance of a vertical through anal fin origin; caudal fin deeply forked; caudal peduncle very slender; penultimate 5–7 vertebrae, in juveniles as well as adults of both sexes, with distal ends of neural and hemal spines flared (anteroposteriorly expanded). Sexual dimorphism exceptionally pronounced, subadult as well as adult males usually with enlarged anal fin, enlarged and pointed or filamentous upper caudal fin lobe, and greatly enlarged humeral spine. Most *Chiloglanis* with 6+6 or fewer mandibular teeth have relatively small suckers and long barbels. No other species has a more slender caudal peduncle, or males with such an elongate upper caudal fin and enlarged humeral spine at such small size. Neural and hemal spines in caudal peduncle slender in all or almost all other species of *Chiloglanis* examined except some larger specimens of *C. occidentalis*.

Coloration in live specimens is recorded in my fieldnotes for two Camerounian localities, high-gradient tributaries of the R. Cross and the R. Nchit, Sanaga basin. Two large Cross specimens had body with dusky, poorly defined bands, almost mottled. Pale areas on body (more distinctly outlined than dusky bands) pale yellowish or dull olivaceous yellow. Caudal fin with dusky vertical bar across base of lobes, light areas pale yellow. Dusky markings on anal fin present but less distinct than in *C. disneyi* collected at same locality. Eye with small oval black pupil, iris dull gray-green. Six specimens from the Nchit (Sanaga) had pale areas on body grayish or olivaceous or pale yellow; alternating dark and pale areas on snout forming in all six specimens a triradiate pattern not evident in specimens of *C. sanagaensis* collected at same locality.

DISTRIBUTION.—*Chiloglanis batesii* probably is the species of *Chiloglanis* with the most extensive distribution. It is found throughout the Niger and Congo basins, in the headwaters of the

Chad basin in Republique Centrafricaine, and in almost every river basin in Cameroun except the Ndian, Nyong, and Ogooué. It occurs sympatrically with six of the nine other species of *Chiloglanis* found in Cameroun.

***Chiloglanis disneyi* Trewavas, 1974**

(Figs. 1e, 2e, 4c, d, 11)

Chiloglanis disneyi Trewavas, 1974:365, figs. 6, 8 (type locality Wowe, Mungo basin, Cameroun).

MATERIAL EXAMINED.—CAMEROUN: BMNH 1973.5.14.342, 34.6 mm, Mungo basin, R. Wowe, Disney collection (holotype); BMNH 1973.5.14:343–344, 2: 23.5–23.8 mm, R. Dilolo, Mungo basin; BMNH 1973.5.1:345, 22.5 mm, R. Blackwater, Mungo basin; CAS 60808, 20: 22.4–31.4 mm, high-gradient streams of R. Cross along road from Mamfe to Bamenda.

Chiloglanis disneyi apparently is a small species, largest specimen only 35 mm (Trewavas 1974:362); sucker moderately large, round; papillae of upper lip with distinctive frond-like margins (Trewavas 1974:365–366, fig. 8); barbels very small; no auxiliary mental barbels; large premaxillary teeth in 3 or 4 rows; mandibular teeth usually in 2 rows, each with 8+8 to 10+10 teeth; eye small; dorsal fin soft rays usually 5 (specimens from Cross basin have 5 in 18, 6 in 2); pectoral fin soft rays 8 or 9; caudal peduncle deep; caudal fin slightly forked, lobes rounded, lower distinctly larger than upper. Secondary sexual dimorphism apparently absent, but largest specimens available lack well-developed gonads.

Live specimens from Cross basin have body with three well-defined, almost black, vertical bands; dorsal surface of head to dorsal fin origin or first dark band on body yellowish orange, orangish brown, or brownish in different individuals; pale bands on body, dorsal, adipose, and caudal fins bright yellow or lemon yellow in all individuals; pectoral, pelvic, and anal fins pale yellow; abdomen off-white or cream; pectoral fin with faint transverse dusky band near its middle; adipose and anal fin base with black spots anteriorly; caudal fin with four large round yellow spots surrounded by sharply defined black marks; eye black. Alternating dark and pale areas on head and body more clearly demarcated in *C. disneyi* than in any other species of *Chiloglanis* observed by me in Cameroun.

DISTRIBUTION.—Known only from Mungo and Cross basins in Cameroun.

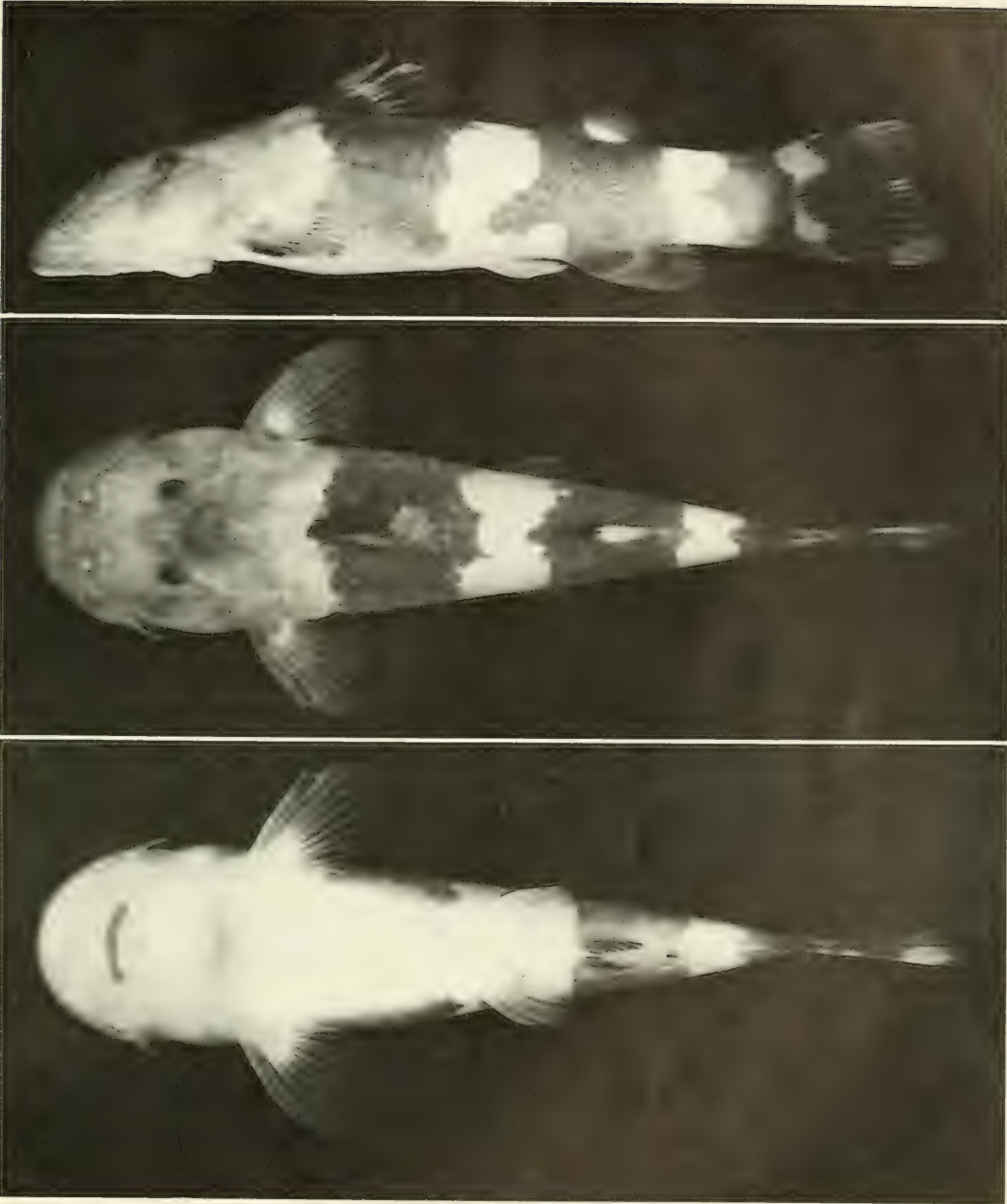


FIGURE 11. *Chiloglanis disneyi*, 31.4 mm (Cross basin).

COMMENT.—I have compared the specimens collected in the Cross with two of Trewavas's specimens collected in the Mungo, and find they agree in most respects. The sucker is relatively larger in the Cross specimens; the smaller suckers of the Mungo specimens may be due to shrinkage in preservative. The color pattern is barely dis-

cernible in the Mungo specimens, which are in poor condition.

***Chiloglanis niger* new species**

(Figs. 1*f*, 2*f*, 4*e*, *f*, 6*f*, 12)

HOLOTYPE.—CAS 60809, 34.4 mm, Cameroun, Niger basin, R. Menchum below high waterfall near Befang, Bamenda highlands, Tyson R. Roberts, 10 Mar. 1980.

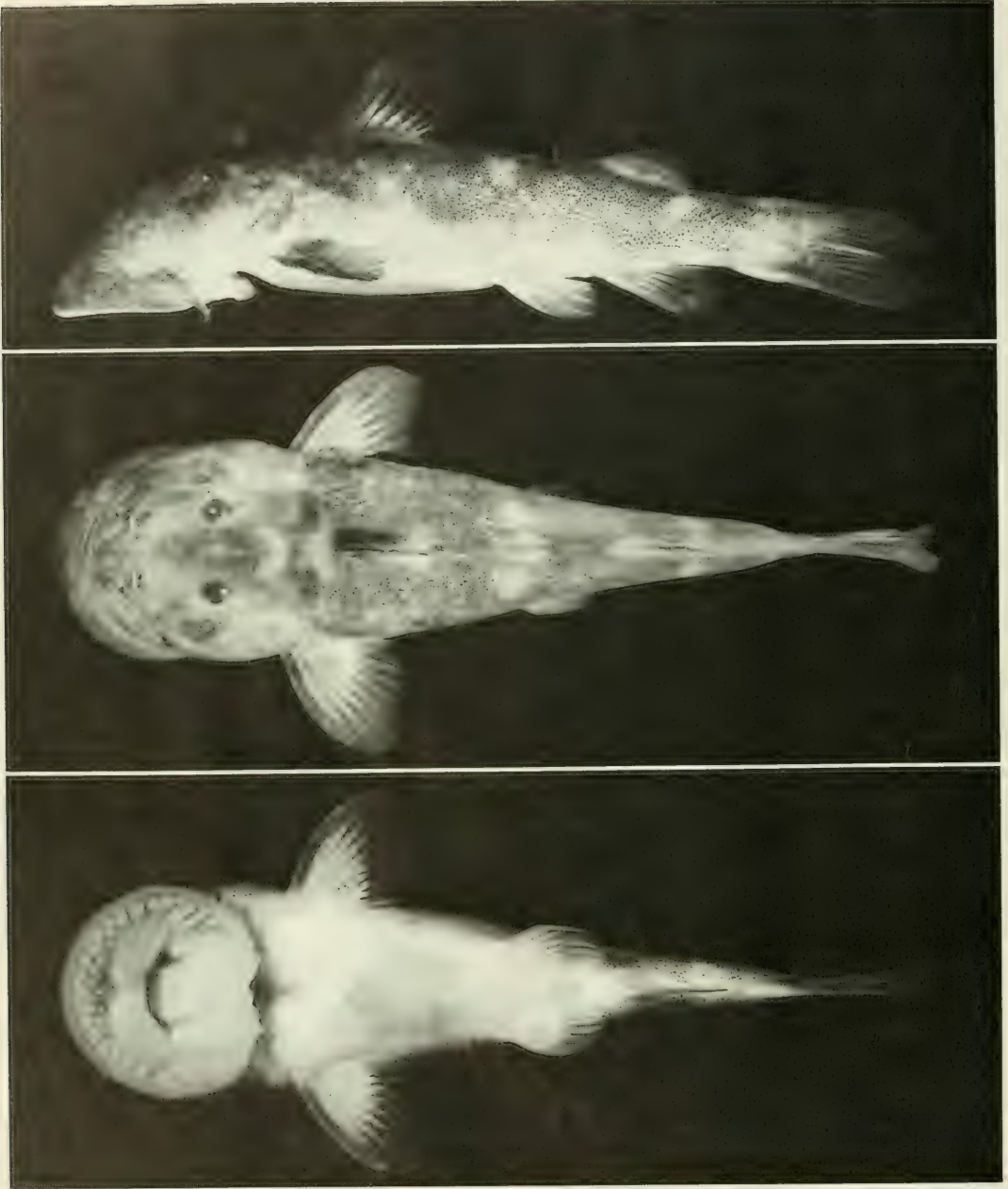


FIGURE 12. *Chiloglanis niger*, holotype, 34.4 mm (Niger basin).

PARATYPES.—CAS 60810, 7: 21.7–35.3 mm, collected with holotype.

Chiloglanis niger (largest known specimen 35.3 mm) has a huge sucker, rounded and somewhat longer than broad; barbels very small; no auxiliary mental barbels; large premaxillary teeth in 7 or 8 rows; mandibular teeth usually in 2 rows;

basic mandibular tooth count 8+8 to 10+10 in largest specimens (6+6 and 7+7 in smallest); eye very small; dorsal fin soft rays 6; pectoral fin soft rays 9 or 10; adipose fin short, its origin only slightly in advance of a vertical through anal fin origin; caudal peduncle slender; caudal fin moderately forked, lobes rounded, equal. No sexual

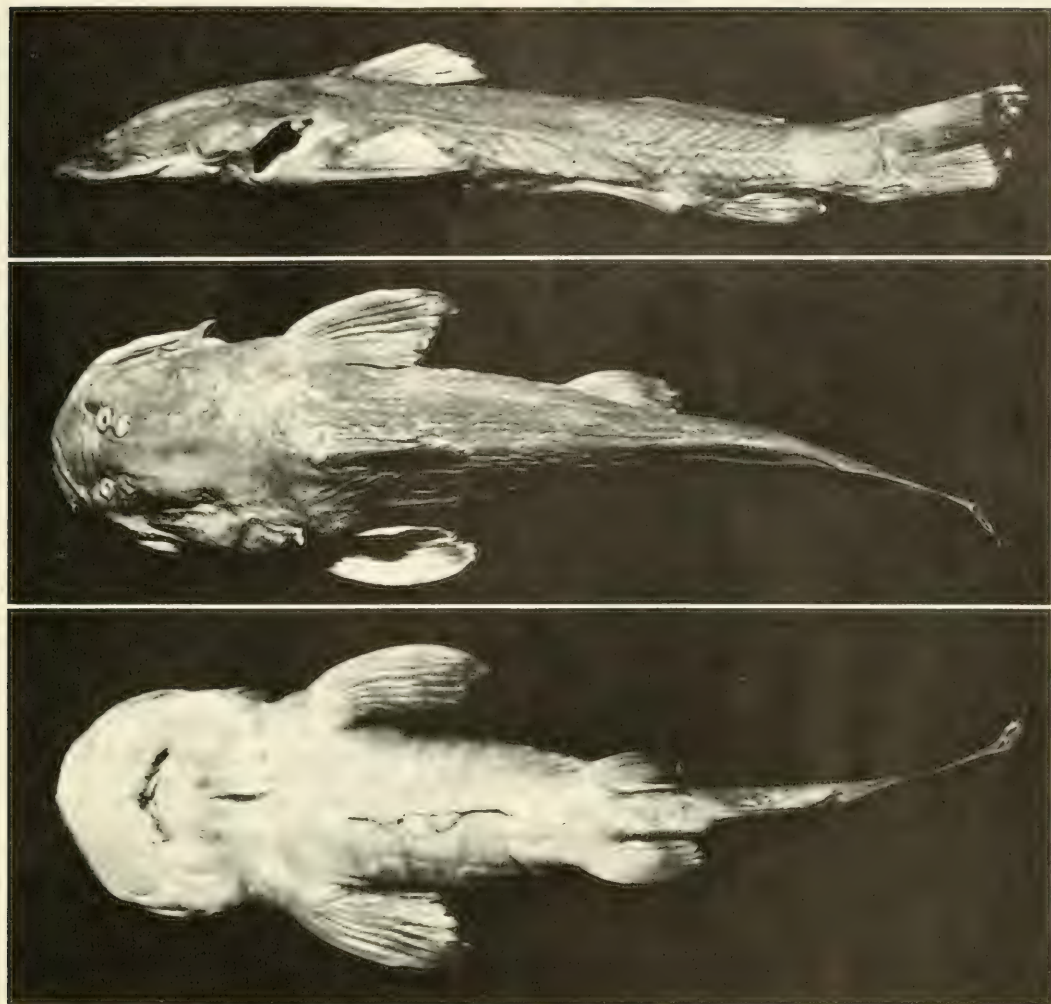


FIGURE 13. *Chiloglanis harbinger*, holotype, immature female 43.5 mm (Lokunje basin).

dimorphism observed (specimens probably immature).

Color of live specimens (collected on a black coarse sand or gravel bottom) uniformly dark, almost black, on entire dorsolateral surface of head and body; abdomen pale. Alternating dark bars and pale intervening areas on body, so typical of species of *Chiloglanis*, but not noted in live fish, faintly discernible preserved specimens.

ETYMOLOGY.—The name *niger* (Latin, black, noun in apposition) refers to the Niger basin as well as to the color in life.

DISTRIBUTION.—Known only from type locality in R. Menchum, Niger basin, Bamenda highlands of Cameroun.

***Chiloglanis harbinger* new species**

(Fig. 13)

HOLOTYPE.—CAS 60811, 43.5 mm immature female, Cameroun, R. Lokunje near Bipindi, A. I. Good, 17 Feb. 1936.

PARATYPES.—CAS(SU) 47469, 9; 34.5–44.0 mm, collected with holotype.

Chiloglanis harbinger (largest specimen 44.0 mm) has a huge sucker, longer than broad; minute barbels; no auxiliary mental barbels; teeth very numerous; large premaxillary teeth in up to 7 rows; mandibular teeth usually in 2 rows, basic mandibular tooth count about 13+13 to 15+15 (teeth of type specimens damaged by string passed through mouth and gills); eye very small; dorsal fin soft rays usually 5 (4 in two specimens); pec-

toral fin soft rays 9 or 10; adipose fin long and low, its origin well in advance of a vertical through anal fin origin; caudal peduncle moderately deep; caudal fin moderately forked, lobes rounded, nearly equal. Males with a moderately elongate genital papilla; no sexual dimorphism observed in size of anal fin, shape of caudal fin, or humeral process of pectoral girdle.

Color in life unknown. Preserved specimens with numerous large melanophores more or less uniformly distributed over entire dorsolateral surface of body; vertical dark bars and intervening pale areas on body (present in most species of *Chiloglanis*) not evident; melanophores extending from sides of body onto sides of abdomen but rapidly becoming sparser toward middle of abdomen (hence very different from uniformly distributed melanophores on abdomen in some specimens of *C. cameronensis*); a dark vertical bar on base of caudal fin as well as one in its middle (very dark area near tip of caudal fin in lateral photograph of holotype an artifact due to shadow from tip of caudal fin, which is broken and bent toward camera).

ETYMOLOGY.—The name *harbinger* (Middle English, noun in apposition) is an allusion to the large number of teeth in the suckermouth mochokid genera *Atopochilus* and *Euchilichthys*, a condition presaged or foreshadowed in this species of *Chiloglanis*.

DISTRIBUTION.—Known only from the Lokunje basin in southeastern Cameroun.

ACKNOWLEDGMENTS

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PROCEEDINGS
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December 20, 1989

AMERICAN DANCE FLIES OF THE
DRAPETIS ASSIMILIS SPECIES GROUP
(DIPTERA: EMPIDIDAE)

By

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ABSTRACT: Eight American species are newly recognized as belonging to the *Drapetis assimilis* species group, including five new species described herein: *Drapetis arnaudi* n. sp. from Florida; *D. cerina* n. sp. from New Mexico; *D. destituta* n. sp. from Baja California; *D. solaris* n. sp. from Mexico (Distrito Federal); and *D. torulosa* n. sp. from Baja California. Lectotypes are designated for *D. latipennis* Melander, 1902 and *D. discalis* Melander, 1918. *Drapetis discalis* Melander is removed from *Crossopalpus* Bigot and redescribed. *Drapetis infumata* Melander is redescribed. A key to American species is provided.

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INTRODUCTION

Flies of the genus *Drapetis* are tiny cursorial predators that are seldom observed or collected. Members of the *D. assimilis* species group have been found on tree trunks and in flowers, and reared from litter in hollow trees; their other habits are unknown.

The *D. assimilis* group was first alluded to by Collin (1961) in discussing characters shared by the Palearctic species, *Drapetis assimilis* Fallén, *D. simulans* Collin, and *D. arcuata* Loew. Subsequently, Kovalev (1972) named and further characterized the group, basing it upon the same three species and *D. ingrica* Kovalev. This classification was followed by Chvála (1975) in a treatment of Scandinavian Tachydromiinae.

The last revision of the American *Drapetis* (Melander 1918) recognized no infrasubgeneric categories, although three members of the *D. assimilis* group were among the 11 valid species

then known. At that time, distinctions among *Drapetis* Meigen, *Crossopalpus* Bigot (= *Eudrapetis* Melander), and *Elaphropeza* Macquart were poorly understood, with the result that for the last 70 years, the American *D. assimilis* group species have been divided between *Drapetis* and *Crossopalpus*. The present paper corrects this unnatural arrangement by uniting the group and placing it within *Drapetis*, s. str.

None of the *D. assimilis* group species have Holarctic distributions, and despite study, none are yet known from the Neotropical Region.

METHODS

Specimens from the following collections were studied. Abbreviations given in parentheses are used in the text to denote depositories: (AC) Collection of the author; (AMNH) American Museum of Natural History; (CAS) California Academy of Sciences; (CIS) University of California

at Berkeley; (CNC) Canadian National Collection; (INHS) Illinois Natural History Survey; (MCZC) Museum of Comparative Zoology; (PHA) Paul H. Arnaud, Jr., Collection; (UCD) University of California at Davis; (UCR) University of California at Riverside; (IUCM) Iowa State University; (UK) University of Kansas; (USNM) United States National Museum of Natural History; (WSU) Washington State University. In listings of materials examined, all collection data preceding a specimen apply to that specimen, unless data that follow are in conflict.

Type specimens of all American species were examined and compared with original descriptions of types and with specimens and descriptions of this study. Descriptions of new species have been based solely on the holotype, with variation among individuals discussed in succeeding paragraphs.

Male genitalia have been drawn in ventrolateral and dorsolateral views, using a camera lucida; wings have been traced from microscope slide projections. Terminology of genitalia follows Griffiths (1972).

Drapetis Meigen

Drapetis Meigen, 1822:91. Type species: *Drapetis exilis* Meigen, 1822 (by monotypy).

A diagnosis of this genus is given elsewhere (Rogers 1983). *Drapetis* is not to be confused with its sister genera, *Crossopalpus* Bigot and *Elaphropeza* Macquart. *Drapetis discalis* Melander was originally described in *Eudrapetis* Melander, a junior synonym of *Crossopalpus*. It, and all species treated here, belong to *Drapetis* Meigen.

Drapetis assimilis Group

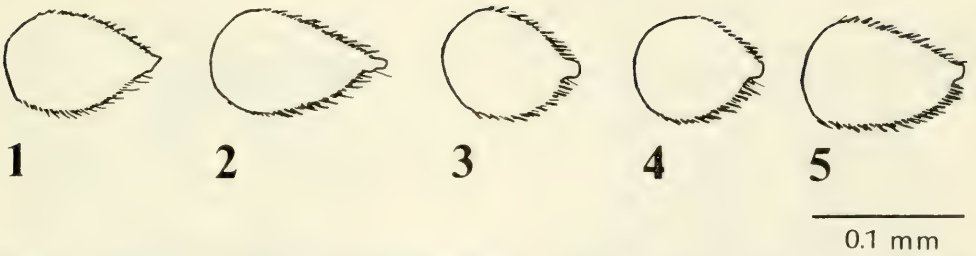
DESCRIPTION.—Males: Head round in frontal view; palpus light to dark brown; antenna uniformly brown, the second segment bearing a distal circlet of setae with one ventral seta longer than all others in the circlet, arista long in relation to the short third segment. Thorax scantily tomentose; when present, propleural tomentum not reaching anterior spiracle; pteropleuron polished; scutellar tomentum invading posterior edge of mesonotum between calli. Wing lacking maculations, veins R_{4+5} and M converging or subparallel distally; second basal (M) cell long, distally extending to below the junction of vein R_1 with the costa; rm crossvein attaching just prox-

imal of center of M cell; mc crossvein perpendicular to Cu or forming a slightly obtuse proximal angle at junction with Cu. Legs long; anterior femur tomentose ventrally; center femur lacking corrugation patterns, ventral surface bearing one or more longitudinal rows of long spines; posterior femur lacking strong anteapical spines on posterior surface; anterior and center tibiae tomentose along flexor surfaces; center tibia lacking a strong apical tooth; posterior tibia lacking true extensor bristles, apical lappet short, blunt, unarmed. Abdomen black, tergites lacking involutions on corners; sclerotization of tergite I interrupted near dorsal midline, other tergites entire; tergites IV and V laterally bearing flattened spines; sternites I, II, III, VI, VII, and VIII entire; sternite IV divided through center; sclerotization of segment VIII narrow and of uniform width dorsally; aedeagus short, concealed within perianthrium. Females: As in males, except all abdominal sternites entire.

The *D. assimilis* group is distinguished from all others by the unique combination of a long projecting seta on the venter of the second antennal segment, a long basal cell, and division of the male abdominal sternite IV. The antennal seta and basal cell have been used before to separate the *D. assimilis* group from other *Drapetis* in keys (Kovalev 1972); the importance of the divided sternite IV has been overlooked.

With the exception of *D. latipennis* Melander, all of the American *D. assimilis* group species have widely polished orbits, and the tomentum of the prothorax fails to reach the anteroventral lateral corner of the humerus. The center tibia bears two parallel rows of short spines along its flexor length in all American species except *D. torulosa* n. sp. Sternite V is divided in a few species, as noted in their respective descriptions.

None of the *D. assimilis* species have the long exerted aedeagus, divided sternite III, wing vein anomalies, nor tibial deformations that appear in various species allied to *D. divergens* Loew. Species related to *D. dividua* Melander have extensor spines on the posterior tibiae and a pedunculate structure articulating with the left perianthrium, both absent in the *D. assimilis* group. Members of the *D. naica* group (Rogers 1983) have an apical thorn on the flexor surface of the center tibia, widely divergent radial and medial veins, a short M cell, and oval head shape. Relatives of *D. exilis* Meigen lack the long ventral



FIGURES 1-5. Third antennal segments of paratype males. Figure 1. *Drapetis arnaudi* n. sp. Figure 2. *Drapetis destituta* n. sp. Figure 3. *Drapetis cerina* n. sp. Figure 4. *Drapetis solaris* n. sp. Figure 5. *Drapetis torulosa* n. sp.

seta on the second antennal segment, present in the *D. assimilis* and *D. naica* groups, and frequently have corrugations on the center femur.

KEY TO SPECIES OF THE *D. ASSIMILIS* GROUP

This key is designed for provisional identification of unmacerated males. Identifications should be confirmed by examination of cleared genitalia. Females are seldom identifiable.

(Males)

- 1. Anterodorsal surface of center femur bulging near proximal quarter, Figure 34; center tibia lacking flexor spines; genitalia, Figures 35, 36 *torulosa* n. sp.
- Anterodorsal surface of center femur shaped normally, Figure 31; center tibia bearing flexor spines 2
- 2. Posterior tibia bearing a group of long, downcurved setae about distal third of extensor surface, Figure 28; genitalia, Figures 29, 30 *latipennis* Melander
- Posterior tibia bearing short setae of nearly uniform length along extensor surface 3
- 3. Setae of anterior surface of center femur directed ventrally, Figure 31; genitalia, Figures 32, 33 *solaris* n. sp.
- Setae of anterior surface of center femur all directed distally 4
- 4. Halter yellow; one pair of vertical bristles 5
- Halter brown; two or three pairs of verticals 6
- 5. Ventral spines of center femur arranged in a single row; propleuron partially tomentose; genitalia, Figures 21-23 *discalis* Melander
- Ventral spines of center femur arranged in two or more rows; propleuron completely

- polished; genitalia, Figures 15, 16 *arnaudi* n. sp.
- 6. Gena obscured by eye in profile; anterior surface of center femur thickly whitish yellow tomentose; two pairs of vertical bristles; genitalia, Figures 17, 18 *cerina* n. sp.
- Gena narrowly visible beneath eye in profile; anterior surface of center femur polished; three pairs of verticals 7
- 7. Bearing a tubercle or a blunt raised projection near posteroventral proximal third of posterior femur; propleuron usually partially tomentose; abdominal tergites VI and VII partially polished; genitalia, Figures 24-27 *infumata* Melander
- Lacking a tubercle or prominence on posteroventral surface of posterior femur; propleuron completely polished; abdominal tergites VI and VII completely tomentose; genitalia, Figures 19, 20 *destituta* n. sp.

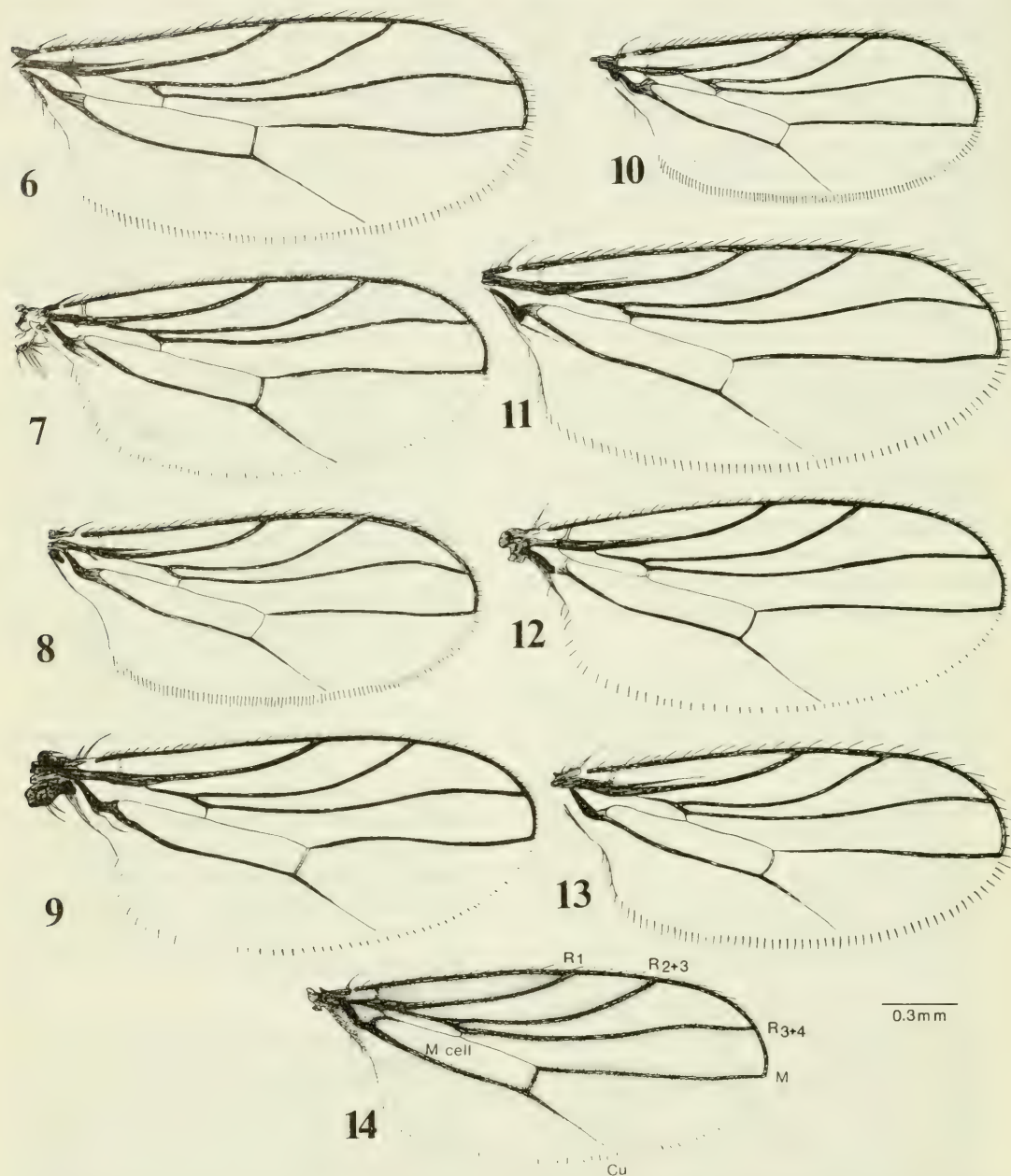
Drapetis arnaudi n. sp.

(Figs. 1, 10, 15, 16)

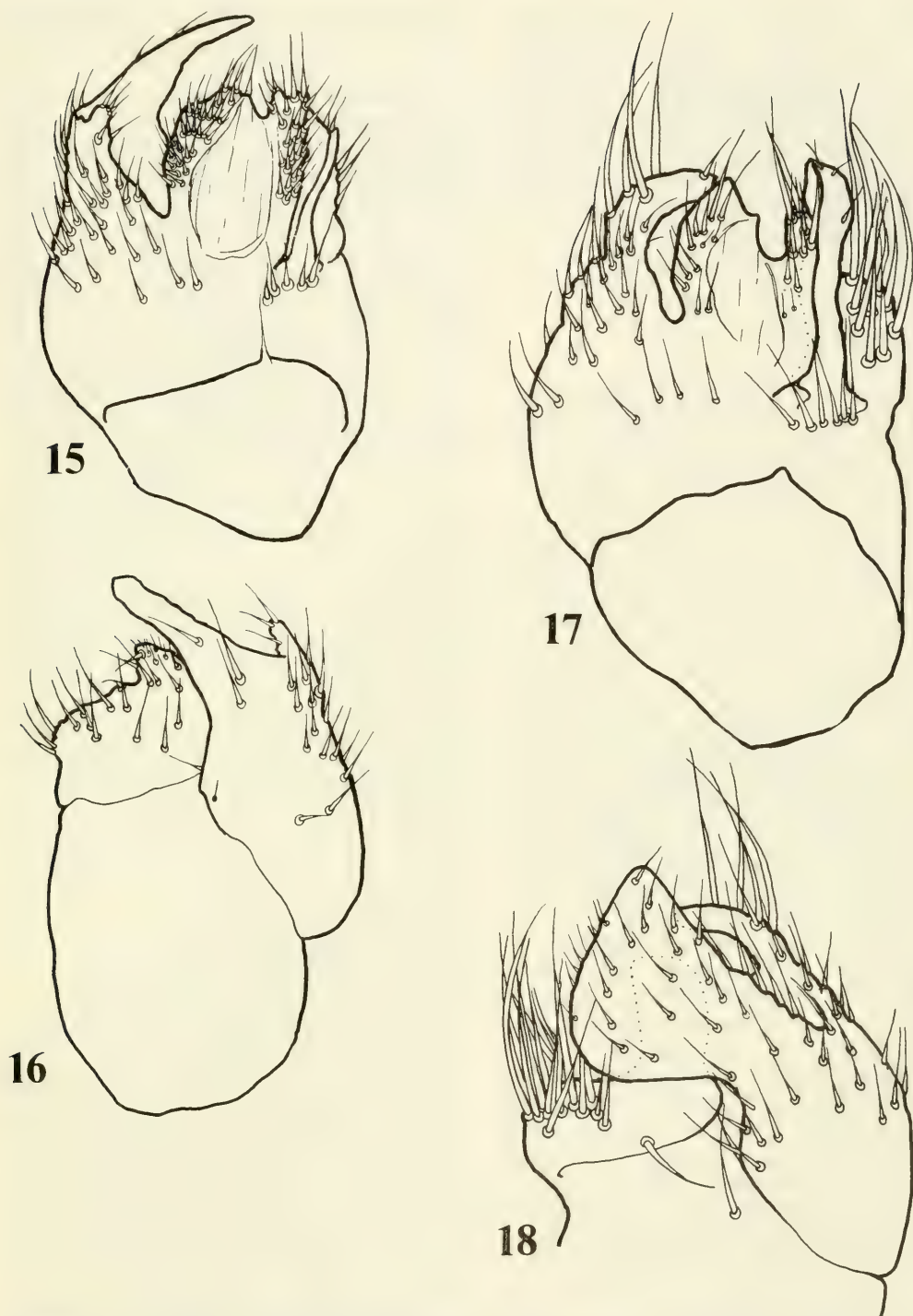
DIAGNOSIS.—One pair of vertical bristles; propleuron completely polished; halter yellow; male genitalia as in Figures 15, 16.

DESCRIPTION.—Male. Length 1.1 mm. Head dark brown; one pair of verticals; frons width at ventral end one-fifth length of third antennal segment; face linear, slightly narrowed toward center; gena entirely visible in profile; third antennal segment shaped as in Figure 1, arista five times its length. Thorax dark brown; propleuron completely polished. Wing 1.3 mm long, neuration as in Figure 10. Legs and coxae bright yellow, ultimate tarsal articles of each leg dark brown. Abdomen laterally bearing tiny flattened spines on segments IV and V.

TYPES.—Holotype: male (CAS 13448), USA:



FIGURES 6-14. Wing venation of males. Figure 6. *Drapetis cerina* n. sp., paratype. Figure 7. *Drapetis discalis*, Brewster Co., Texas. Figure 8. *Drapetis torulosa* n. sp., paratype. Figure 9. *Drapetis latipennis*, Orange Co., California. Figure 10. *Drapetis arnaudi* n. sp., paratype. Figure 11. *Drapetis solaris* n. sp., paratype. Figure 12. *Drapetis discalis*, Riverside Co., California. Figure 13. *Drapetis destituta* n. sp., paratype. Figure 14. *Drapetis infumata*, Chelan Co., Washington.



FIGURES 15-18. Genitalia of male paratypes. Figures 15 (ventrolateral view) and 16 (dorsolateral view). *Drapetis arnaudi* n. sp. Figures 17 (ventrolateral view) and 18 (dorsolateral view). *Drapetis cerina* n. sp.

labelled, "FLA: Highlands Co., Archbold Biol. Sta., 7.X.1964, P. H. Arnaud, Jr." Paratypes, same locality: 2 males, 10.X.1964 (CAS and AC), 1 male, 7.X.1964 (CAS), 1 male, 12.X.1964 (AC).

REMARKS.—The paratypes have three rows of ventral spines on the center femur, merging distally into two rows, not visible on the holotype. The posterior femur bears a single row of poorly developed ventral setae.

This species is named for its collector, Dr. Paul H. Arnaud, Jr.

***Drapetis cerina* n. sp.**

(Figs. 3, 6, 17, 18)

DIAGNOSIS.—Two pairs of vertical bristles; gena obscured by eye in profile; halter brown; anterior surface of center femur whitish yellow tomentose; male genitalia as in Figures 17, 18.

DESCRIPTION.—Male. Length 1.8 mm. Head black; two pairs of verticals, outer pair short; frons width at ventral end one-seventh length of third antennal segment; face linear; gena obscured by eye in profile; third antennal segment shaped as in Figure 3, arista six times its length. Thorax black; one weakly developed humeral bristle; propleural tomentum present, narrowly failing to reach anteroventral lateral corner of humerus; halter dark brown. Wing 2.0 mm long, neuration as in Figure 6. Legs and coxae yellow, with a brownish cast in coxae and tarsi; anterior surface of center femur completely coated with translucent, waxy, whitish yellow tomentum, ventral surface bearing brown spines set in two irregular rows, spines longest near centers of rows; flexor spines of center tibia very poorly developed; posterior femur with one row of ventral setae and four long anteroventral distal bristles near knee. Abdomen laterally bearing erect flattened spines on tergites IV and V.

TYPES.—Holotype: male (USNM 762713), USA: labelled, "Las Vegas HS, 14.5, NM, H. S. Barber Collector." Paratype: 1 male, USA: New Mexico: Santa Fe Co., Santa Fe, VII (USNM).

REMARKS.—The anterior surface of the center femur looks much as though it were smeared with wax, producing greasy reflections. The adjective *cerina* refers to this waxy quality.

***Drapetis destituta* n. sp.**

(Figs. 2, 13, 19, 20)

DIAGNOSIS.—Three pairs of strong vertical bristles; propleuron completely polished; halter

dark brown; abdominal tergites VI and VII completely tomentose; male genitalia as in Figures 19, 20.

DESCRIPTION.—Male. Length 14 mm. Head black; three verticals; frons width at ventral end one-sixth length of third antennal segment; face linear; gena entirely visible in profile; third antennal segment shaped as in Figure 2, arista four times its length. Thorax dark brown; propleuron completely polished; halter dark brown. Wing 1.6 mm long, neuration as in Figure 13. Legs and coxae yellow, except tarsi and posterior knees brown; center femur bearing two rows of strong, dark brown ventral spines, merging distally into one row at about half length, continuing along entire femur; posterior femur bearing two rows of long yellow setae along entire length, one row anteroventral, the other posteroventral. Abdomen laterally bearing long flattened spines on tergites IV and V; tergites VI and VII completely tomentose.

TYPES.—Holotype: male (CAS 13451), MEXICO: labelled, "MEXICO: Baja California: Agua Caliente (San Carlos), 18.5 km east of Maneadero, 6.VII.1973, Paul H. Arnaud, Jr." Paratype: 1 male, same data (PHA).

REMARKS.—Maceration of the paratype reveals that abdominal sternite V is divided. Recognition of this species relies primarily on genitalic differences; it lacks other unique characteristics.

***Drapetis discalis* (Melander)**

(Figs. 7, 12, 21–23)

Eudrapetis discalis Melander, 1918:198.

Drapetis (*Eudrapetis*) *discalis*; Melander, 1928:310.

Drapetis (*Crossopalpus*) *discalis*; Melander, 1965:477.

DIAGNOSIS.—One pair of vertical bristles; male genitalia as in Figures 21–23.

REDESCRIPTION.—The original description will suffice to recognize *D. discalis* with the following corrections based on the lectotype: body shining brown; halter yellowish-clear; second, third, and fourth sections of costa proportioned 2.4:2.8:8.1; rm crossvein at five-twelfths of the length of second basal cell; outer two sections of vein M_{1+2} proportioned 1:2.

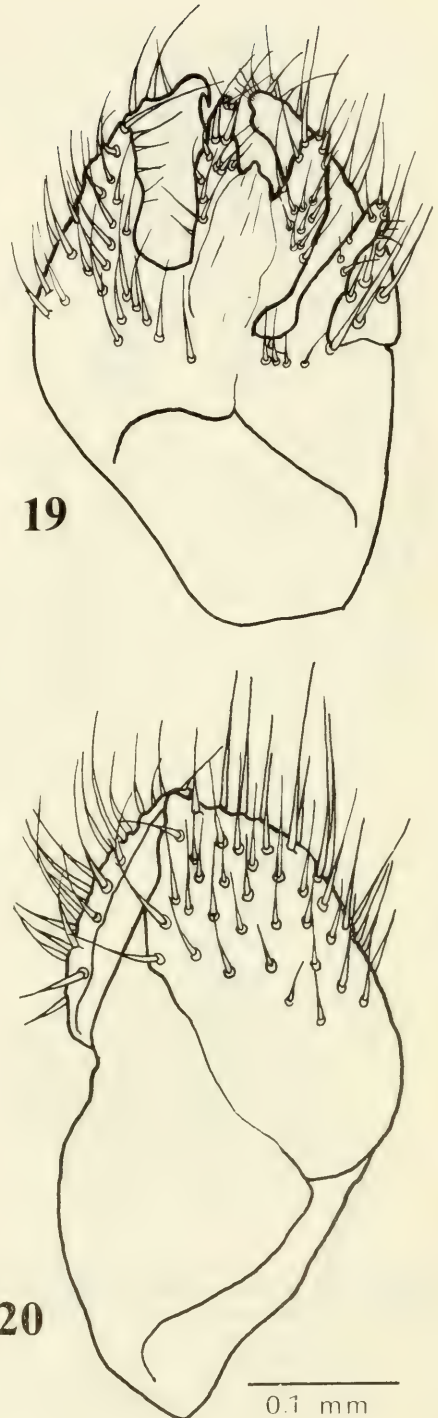
TYPES.—Melander labelled his Washington specimen "type," and his California specimen "paratype," but neglected to publish a designation of the holotype. Lectotype male (USNM), here designated, USA: labelled, "Wawawai Wash

22.VI." Paralectotype male (USNM), USA: California: Santa Clara Co., Palo Alto.

OTHER MATERIAL EXAMINED.—USA: **California:** Contra Costa Co., 1 male, Orinda Village, 18.VI.1970, E. I. Schlinger (AC); Monterey Co., 3 males, 25.IX.1934, A. L. Melander (USNM), 1 male, 8 km SW Greenfield, 3.V.1975, P. A. Rude (AC), 1 male, Soledad, 20.V.1956, H. R. Moffitt (UCD); Orange Co., 1 male, 14.VI.1929, P. W. Oman (UK); Riverside Co., 1 male, 8 km S of Sage, 16.IV.1965, C. A. Toschi (CIS), 2 males, Whitewater Cyn., 11.IV.1965, J. T. Doyen (CIS); San Bernardino Co., 1 male, Loma Linda, 13.V.1953, R. E. Ryckman (USNM), 1 male, Upper Santa Ana River, 28.IX.1953, A. L. Melander (USNM), 1 male, Mountain Home Cyn., 27.IX.1955, A. L. Melander (USNM), 1 male, Verdemon, 1.V.1946, A. L. Melander (USNM); San Diego Co., 1 male, 4.8 km WSW of Escondido, 23.III.1975, P. A. Rude (AC); Santa Barbara Co., 1 male, Santa Barbara, 16.VI.1951, K. W. Tucker (UCD); Santa Clara Co., 2 males, Los Gatos, off Stacia Street, *Quercus* trunk, 30.V/23.VII.1977, E. J. Rogers (AC), 5 males, Stanford, 19.XI.1952, P. H. Arnaud (PHA); Shasta Co., 1 male, McArthur, 12.X.1952, E. I. Schlinger (UCD); Ventura Co., 1 male, Saticoy, 5.V.1924, S. E. Flanders (CAS). **Idaho:** Nez Perce Co., 1 male, Lewiston Hill, 31.V.1924, A. L. Melander (USNM), 1 male, 30.VI.1975, E. J. Rogers (AC). **Texas:** Brewster Co., 2 males, Panther Junction, Big Bend Nat'l. Park, 1,067 m, 14.V.1959, J. F. McAlpine (CNC); Gillespie Co., 1 male, Pedernales River, 4.IV.1955, W. W. Wirth (USNM); San Patricio Co., 1 male, Padres Id. near Port Aransas, 23.III.1965, J. G. Chillcott (CNC). **Utah:** Cache Co., 1 male, Blacksmith Fork Cyn., 11.VIII.1975, G. F. Knowlton (UCD). **Washington:** Asotin Co., 1 male, Fields' Spring State Park, 31.VII.1971, W. J. Turner (WSU), 1 male, 27.4 km S of Anacostone, 594 m, fls. *Lonicera*, 15.IV.1977, W. J. Turner (WSU); Whitman Co., 3 males, Yakawawa Cyn., 11.3 km NW of Colton, 762 m, 25/27.VI.1977, W. J. Turner (WSU), 1 male, Big Almota Cyn., Almota, 25.VII.1973, D. Corredor and S. Berkenkamp (WSU). **MEXICO: Baja California:** 1 male, 9 km E of Hamilton Ranch Arr. Santo Domingo, 23.IV.1963, H. B. Leech and P. H. Arnaud (CAS).

REMARKS.—The gena is usually narrowly visible in profile (not in specimens from Brewster Co., Texas). The ventral half of the propleuron is usually tomentose (completely polished in all Texas specimens). Most individuals show a single, poorly distinguishable humeral bristle. The halter may be yellow or (rarely) brown. Ventral spines of the center femur are arranged in a single row, and the posterior femur bears a ventral row of setae. Abdominal sternite V is divided.

Distinguishing between *D. discalis* and *D. infumata* Melander is difficult. Cerci of the two species vary widely in shape (Figs. 21, 22, 24, 25), and Pacific Coast *D. discalis* occasionally have brown halteres, or infumated wings, or have the mc crossvein located proximad of the junction of vein R_1 with the costa, all as in *D. infumata*. Difference in the number of vertical bristles appears to be the best character for separation.

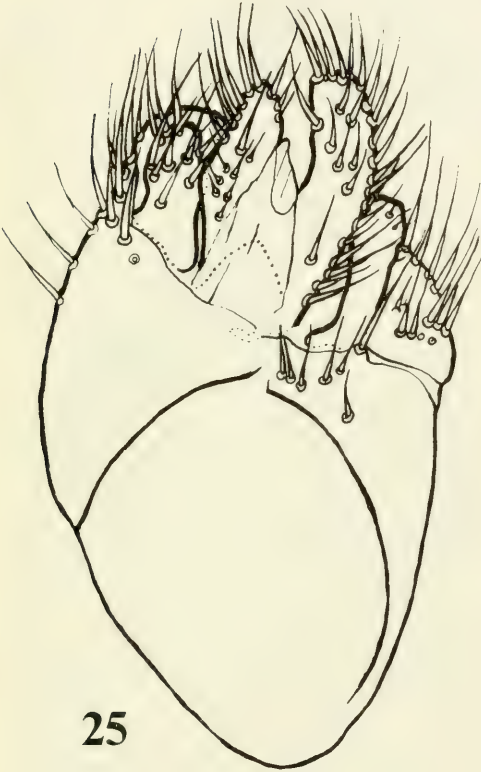
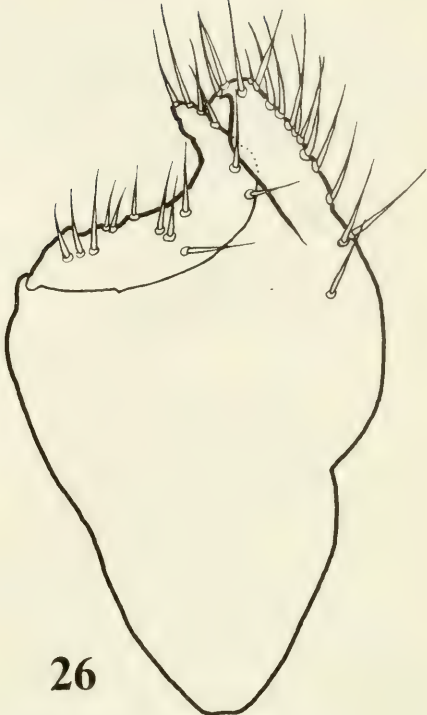


FIGURES 19, 20. Genitalia of paratype male *Drapetis dituta* n. sp. Figure 19. Ventrolateral view. Figure 20. Dorso-lateral view.



FIGURES 21-23. Genitalia of male *Drapetis discalis*. Figure 21 (ventrolateral view). Brewster Co., Texas. Figure 22 (ventrolateral view). Cerci, Monterey Co., California. Figure 23 (dorsolateral view). Santa Clara Co., California.

FIGURES 24-27. Genitalia of male *Drapetis infumata*. Figure 24 (ventrolateral view). Cerci, Chelan Co., Washington. Figure 25 (ventrolateral view). Monmouth Co., New Jersey. Figure 26 (dorsolateral view). Chelan Co., Washington. Figure 27 (dorsolateral view). Monmouth Co., New Jersey.



Eudrapetis Melander (1918) is an obvious synonym of *Crossopalpus* Bigot (1857). *Crossopalpus* have produced genae, a single pair of ocellar bristles, and lack mesopleural setae. Like other *Drapetis*, *D. discalis* has short genae, two pairs of ocellars, and hairy mesopleurae.

Drapetis infumata Melander

(Figs. 14, 24–27)

Drapetis latipennis Melander, 1902:209 (in part, male paratype from Milwaukee, Wisconsin).

Drapetis infumata Melander, 1918:194.

Drapetis naica Melander, 1918:195 (in part, male paratype from Avon, Idaho).

DIAGNOSIS.—Three pairs of strong vertical bristles; a gentle prominence or pointed tubercle near posteroventral proximal third of posterior femur; male genitalia as in Figures 24–27.

REDESCRIPTION.—Males. Length 1.2 to 1.5 mm. Head dark brown; three pairs of verticals; frons width at ventral end one-third to one-fifth length of third antennal segment. Thorax black to brown; one weak humeral bristle; propleural tomentum present, not attaining anteroventral lateral corner of humerus nor anterior spiracle; halter dark brown. Wing 1.6 to 1.9 mm long, occasionally infumated along veins, mc crossvein located proximad to junction of R_1 with costa, Figure 14. Legs and coxae dark yellow to dark brown, anterior femur and coxa and proximal areas of other femora lightest colored; center femur bearing a single row of ventral spines; posterior femur bearing one row of posteroventral setae along distal half, one row of short to long setae along entire ventral length, and a posteroventral tubercle or node near proximal third. Abdomen laterally bearing tiny flattened spines on tergites IV and V, closely appressed to body; abdominal sternite V usually divided; genitalia as in Figures 24–27.

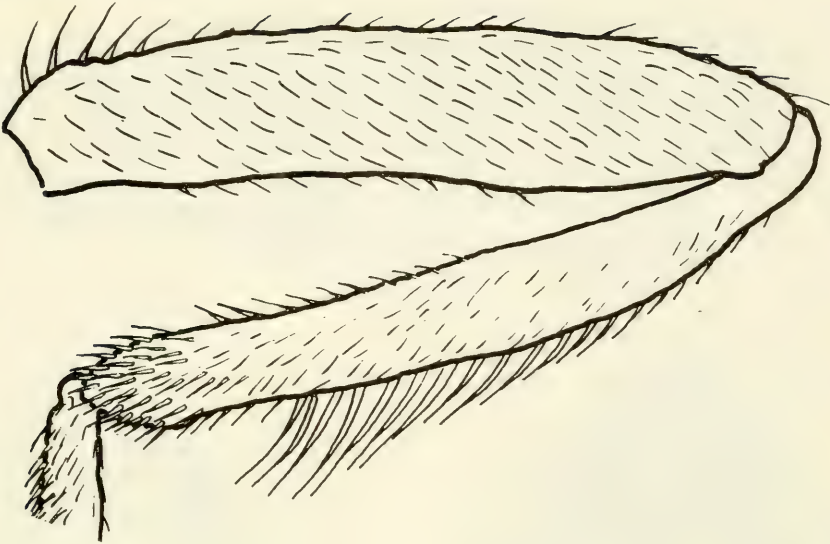
Types—Holotype (*D. infumata*): female (USNM), CANADA: labelled, "Nelson, British Columbia." Paratype (*D. infumata*) female (USNM), USA: Priest Lake, Bonner Co., Idaho (may be one of two females from Priest Lake, collected 1.VIII.1916, but lacking a type label). Paratype (of *D. latipennis*) male (AMNH 729), USA: Milwaukee, Wisconsin, 23.VI.1895, W. M. Wheeler. Paratype (of *D. naica*) male, USA: Avon, Idaho (USNM).

OTHER MATERIAL EXAMINED.—USA: California: El Dorado Co., 1 male, Blodgett Forest, 21 km E Georgetown,

12.VIII.1975, P. A. Rude (AC); Humboldt Co., 1 male, Willow Creek, 12.VIII.1948, W. W. Wirth (USNM); Madera Co., 1 male, SE slope of Green Mtn., 2,316 m, 20.VIII.1971, H. B. Leech (CAS); Mono Co., 1 male, 8 km N Bridgeport, Huntton Forest Camp, 2,073 m, 22.VIII.1966, P. H. Arnaud (AC); Siskiyou Co., 1 male, Poker Flat, 1,536 m, 13.VIII.1966, H. B. Leech (CAS); Tuolumne Co., 1 male, Pinecrest, 11.VIII.1948, P. H. Arnaud (PHA). **Georgia:** Dade Co., 1 male, Cloudland Cyn. State Park, 8.V.1952, O. Peck (CNC). **Idaho:** Kootenai Co., 1 male, Carlin Bay, Lk. Coeur d'Alene, 16 km N of Harrison, 640 m, 14/20.VII.1981, W. J. Turner (AC), 1 male, 21/23.VIII.1977 (WSU), 1 male, 24/28.VII.1977 (WSU); Latah Co., 42 males, Lost Creek, 19.3 km ENE of Potlatch, 823 m, 5.VIII.1979, W. J. Turner (WSU), 6 males (AC), 1 male, 1.VII.1980 (WSU), 1 male, 7.VII.1980 (WSU), 1 male (AC), 7 males, 23.VII.1980 (WSU), 1 male (AC), 2 males, Styrcrhine Creek, 24.1 km ENE Potlatch, 884 m, 1/3.VII.1980 (WSU), 1 male, 7/9.VII.1980 (WSU), 1 male, *Physocarpus*, 1.VII.1980 (WSU), 4 males, 11.3 km NNE of Moscow, 823 m, 24.VII.1980, W. J. Turner (WSU), 5 males, Big Meadow Rec. Area, 11.3 km N of Troy, 914 m, 31.VII.1979, W. J. Turner (WSU), 3 males (AC), 1 male, L. Sand Creek nr. Bonami Creek, 25.7 km E of Potlatch, 884 m, 9.VIII.1979, W. J. Turner (WSU). **Iowa:** Boone Co., 1 male, Ledges State Park, 23.VI.1961, J. L. Laffoon (UICM). **Michigan:** Midland Co., 1 male, 5.VII.1951, R. R. Dreisbach (USNM). **New Jersey:** Monmouth Co., 1 male, Long Branch, 11.VI., C. W. Johnson (MCZC). **Oregon:** Baker Co., 3 males, Up. Goose Creek, 54.7 km SE of Union, 1,268 m, 13/19.VII.1975, E. J. Davis (WSU), 1 male (AC), 1 male, Low. Goose Creek, 57.9 km SE of Union, 1,219 m, 13/19.VII.1975, E. J. Davis (WSU), 1 male, Velvet Creek, 22.1 km SE of Union, 1,439 m, 13/19.VII.1975, E. J. Davis (AC); Grant Co., 1 male, 40 km N Mt. Vernon, 24.VII.1974, P. H. Arnaud (CAS); Union Co., 1 male, Low. Lick Creek, 41.8 km SE of Union, 1,305 m, 21/23.VII.1977, E. J. Davis (WSU). **Virginia:** Montgomery Co., 1 male, Blacksburg, 640 m, 28.VI.1962, J. G. Chillcott (AC); Roanoke Co., 1 male, Mt. Roanoke, 18.V.1965, J. G. Chillcott (AC). **Washington:** Asotin Co., 1 male, 6.4 km S of Anatone, 1,097 m, 12.VIII.1980, W. Turner (WSU), 1 male, Fields' Spring State Park, 1,067–1,219 m, 30.VI.1975, W. J. Turner (WSU); Chelan Co., 1 male, Lucerne, 29.VIII.1919, A. L. Melander (USNM). **CANADA:** **Manitoba:** 1 male, Ninette, "*Betula glandulosa*, *Populus balsamifera* associate," 15.VII.1958, J. G. Chillcott (CNC). **Ontario:** Ottawa, 1 male, 26.VI.1958, J. G. Chillcott (AC), 1 male, 9.VI.1962, J. R. Vockeroth (CNC), 1 male, Maynooth, 22.VI.1953, J. F. McAlpine (CNC). **Quebec:** 1 male, Old Chelsea, Summit King Mtn., 351 m, 25.VI.1962, J. R. Vockeroth (CNC), 1 male, 9.VIII.1961 (CNC). **Saskatchewan:** 1 male, Uranium City, 59°34'N 108°36'W, 18.VI.1962, J. G. Chillcott (CNC), 1 male, Wallwort, 52°33'N 104°03'W, 20.VII.1942, J. D. Ritchie (UK).

REMARKS.—Development of the ventral setae and tubercle of the posterior femur shows considerable variation. Specimens from the Atlantic Coast have long setae, a distinct nipple-like tubercle, and genitalia confirming substantially to Figures 25 and 27. Specimens collected between Ontario and California have short setae, and more often a gentle prominence rather than a tubercle, with genitalia resembling Figures 24 and 26. Cal-

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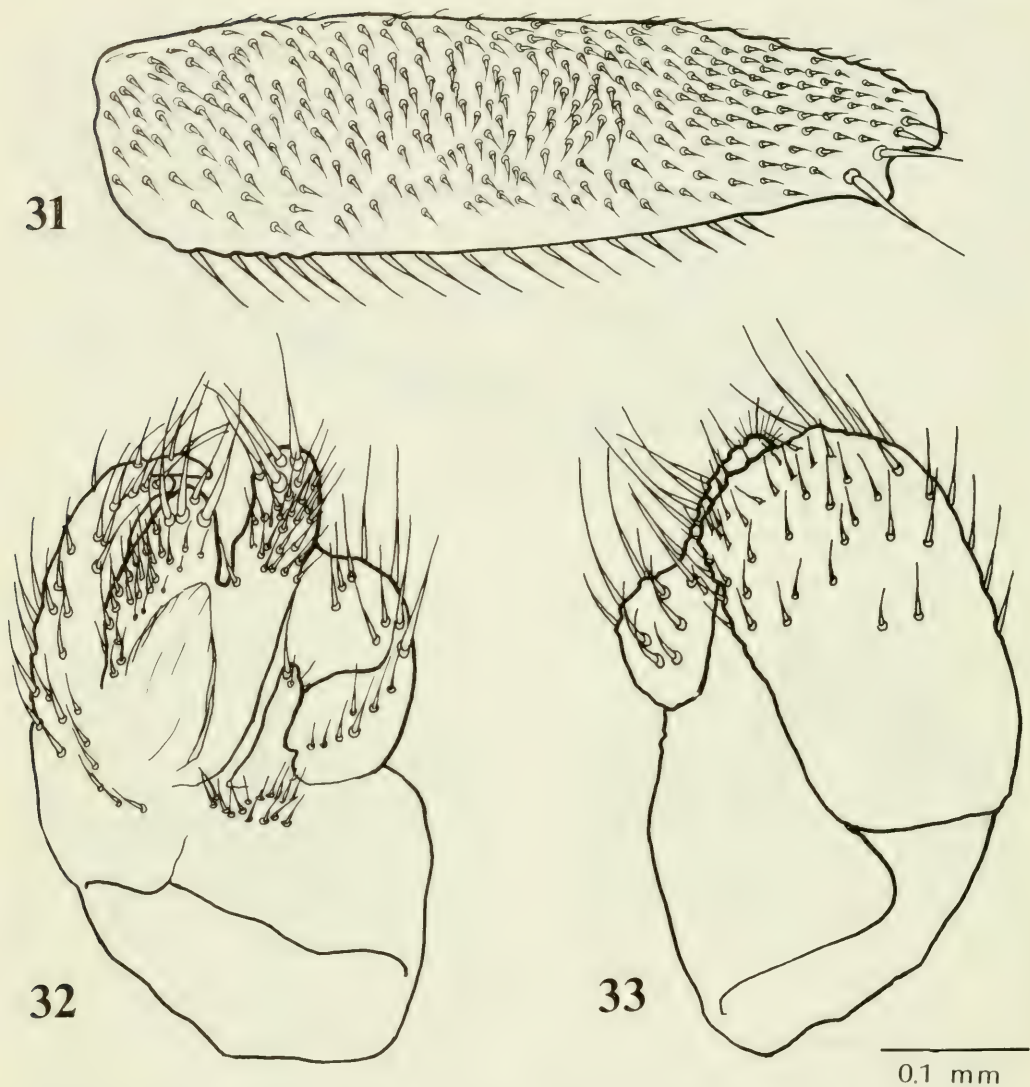
30



FIGURES 28–30. *Drapetis latipennis*. Figure 28. Posterior view of male hind leg, Douglas Co., Kansas. Figures 29 (ventrolateral view) and 30 (dorsolateral view). Male genitalia, Orange Co., California.

ifornia material often shows well-developed tubercles and genitalia similar to Atlantic Coast specimens. Abdominal tergites VI and VII are mostly polished in specimens from Lost Creek,

Idaho. Specimens from Velvet Creek, Oregon, and Coeur d'Alene Lake, Idaho, lack all propleural tomentum. Sternite V is undivided in specimens from Big Meadow Creek, Idaho.



FIGURES 31-33. *Drapetis solaris* n. sp., paratype male. Figure 31. Anterior view of femur of center leg. Figures 32 (ventrolateral view) and 33 (dorsolateral view). Genitalia.

Individuals from the Pacific Coast have so far been collected only in mountainous regions, where wing infumation occurs only sporadically and is coincident with generalized melanism.

***Drapetis latipennis* Melander**

(Figs. 9, 28-30)

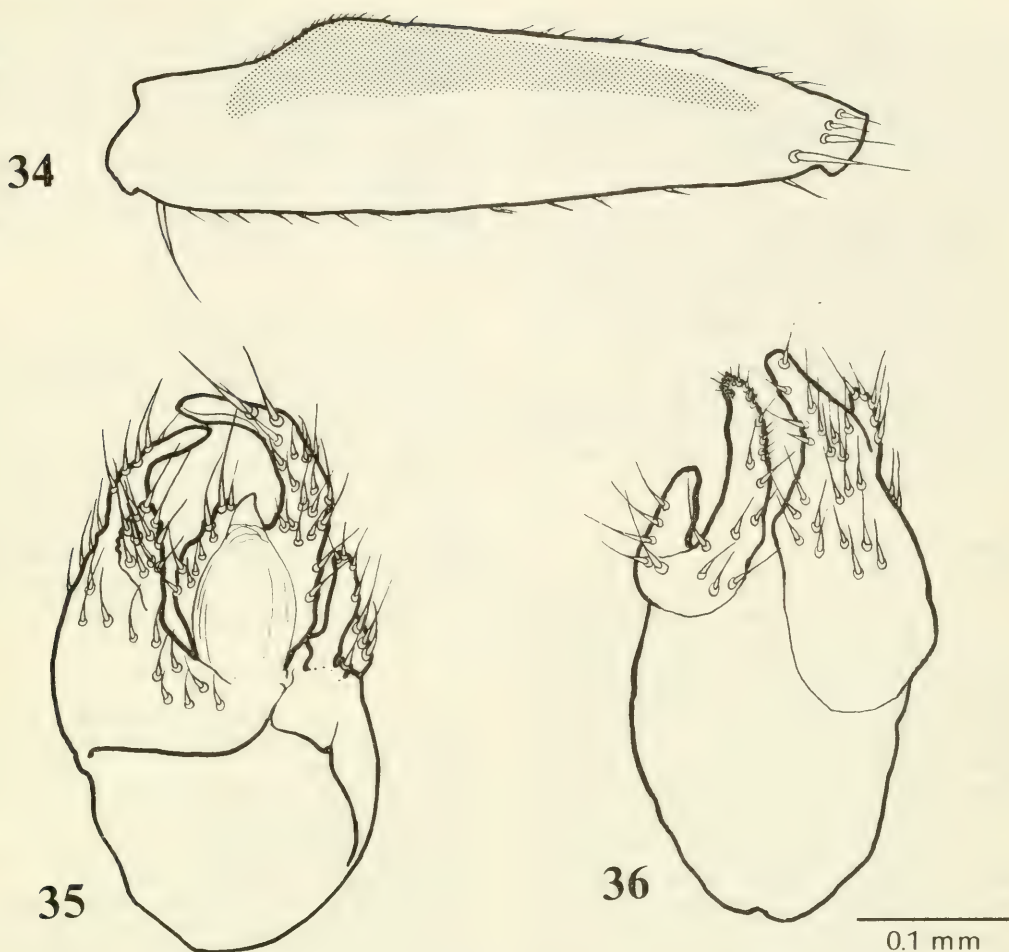
Drapetis latipennis Melander, 1902:209.

DIAGNOSIS.—Three strong pairs of verticals; gena obscured by eye in profile; propleural tomentum profuse, extending to anteroventral lateral corner of humerus; posterior femur bearing

five to seven long, sturdy anteroventral bristles along distal quarter; posterior tibia bearing a group of long, downturned setae near distal third of extensor surface; genitalia as in Figures 29, 30.

TYPES.—Lectotype (here designated): male (USNM), USA: labelled, "Lawrence Kans." Paralectotypes, same locality: 1 male (USNM), 3 females (AMNH 730). A male from Milwaukee, Wisconsin (AMNH 729) included in the original type series is *Drapetis infumata*.

OTHER MATERIAL EXAMINED.—USA: **California:** Orange Co., 2 males, Irvine Ranch nr. Bonita Creek., "on *Platanus*," 24.V.1963, E. I. Schlinger (UCR). **Illinois:** Champaign Co., 1



FIGURES 34-36. *Drapetis torulosa* n. sp., paratype male. Figure 34. Anterior view of center leg. Tomentose area indicated by stippling. Figures 35 (ventrolateral view) and 36 (dorsolateral view). Genitalia.

male, Urbana, 29.VI.1915 (IHNS). **Kansas:** Douglas Co., 1 male, Atherton (USNM). **New York:** Ulster Co., 1 male, Cherrytown, 8/18.VIII.1971, P. and B. Wygodzinsky (AMNH).

REMARKS.—Flattened spines of abdominal tergites IV and V are long, thick and erect. The peculiar long setae on the posterior tibia are present in both sexes, but are shorter in females; *Drapetis assimilis* Meigen has less developed long setae in the same location.

***Drapetis solaris* n. sp.**

(Figures 4, 11, 31-33)

DIAGNOSIS.—Center femur bearing ventrally directed setae across center of anterior surface, Figure 31; genitalia as in Figures 32, 33.

DESCRIPTION.—Male. Length 1.6 mm. Head black; three pairs of verticals, outer two short; frons width at ventral end one-sixth length of third antennal segment; face linear; gena entirely visible in profile; third antennal segment shaped as in Figure 4, arista seven times its length. Thorax black, except posterior edge of mesopleuron and dorsal edge of sternopleuron dark brown; humerus bearing an inconspicuous bristle; propleural tomentum limited to ventral margin; halter light brown. Wing 1.6 mm long, neuration as in Figure 11. Legs and coxae chiefly dark brown, slightly lighter at knees, on tarsal articles and anterior tibia, and in ventral half of anterior coxa; center femur bearing a single row of ventral spines along entire femoral length, spines longer proxi-

mally, anterior surface of femur bearing ventrally directed setae and an unusually sturdy anteroventral distal bristle; center tibia very slightly bowed; a row of very long ventral setae along entire length of posterior femur. Abdomen laterally bearing long, flattened spines on tergites IV and V.

TYPES.—Holotype: male (CAS 13455), MEXICO: labelled, "MEXICO: Mexico: Teotihuacan Pyramid to the Sun. 27.XII.1970, P. H. and M. Arnaud/Coll. at flowers *Cassia tomentosa* L.f. Fam. Leguminosae Det. D. Breedlove." Paratypes: 3 males, same data (CAS).

REMARKS.—The face of one paratype is constricted ventrally, and another has no discernible outer vertical. The species is named in reference to its type locality.

***Drapetis torulosa* n. sp.**

(Figs. 5, 8, 34–36)

DIAGNOSIS.—Three pairs of strong verticals; anterodorsal surface of center femur with a tomentose callosity erupting at proximal quarter and gradually subsiding distally, Figure 34, posteroventral surface bearing one row of bristles, bristles lengthening distally; center tibia lacking flexor spines; genitalia as in Figures 35, 36.

DESCRIPTION.—Male. Length 1.4 mm. Head black; three pairs of verticals; frons width at ventral end one-eighth length of third antennal segment; face strongly constricted at ventral end; gena entirely visible in profile; third antennal segment shaped as in Figure 5, arista five times its length. Thorax dark brown; propleuron completely polished, three weak pale setae along vertical suture; halter dark yellow. Wing 1.6 mm long, neuration as in Figure 8. Legs and coxae yellow, except tarsi yellowish brown; center femur with one very strong, nearly erect anteroventral distal bristle near knee, and strong yellow posteroventral bristles in a single row, bristles lengthening distally along proximal three-quarters of femur; anterodorsal surface of center femur thickly tomentose, with a long swelling beginning at proximal quarter and distally subsiding across remaining length of femur; center tibia lacking flexor spines; posterior femur lacking ventral setae, bearing a rounded basal lump on posteroventral surface just distad of trochanter. Abdomen laterally bearing tiny flattened spines on tergites IV and V, closely appressed to body.

TYPES.—Holotype: male (CAS 13459), MEXICO: labelled, "MEXICO: Baja California: Agua Caliente (San Carlos), 18.5 km east of Maneadero, 6.VII.1973, Paul H. Arnaud, Jr." Paratypes, same data, 1 male (AC), 2 males (PHA).

REMARKS.—Abdominal sternite V of a macerated paratype is divided through the center. This species is named in reference to the peculiar modification of the center femur.

ACKNOWLEDGMENTS

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December 20, 1989

ECOLOGICAL, EVOLUTIONARY, AND CONSERVATION
IMPLICATIONS OF FEEDING BIOLOGY IN OLD WORLD
CAT SNAKES, GENUS *BOIGA* (COLUBRIDAE)

By

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ABSTRACT: Cat snakes forage actively and sometimes consume multiple prey items at a site. Some species use an unusual style of constriction and venom to immobilize prey, which is typically swallowed head-first. Approximately 300 prey items from 21 species demonstrate intra- and interindividual, ontogenetic, and geographic dietary variation. Most species of *Boiga* are small to moderately long snakes that eat mainly lizards, or large snakes that eat lizards as juveniles and mainly mammals and/or birds as adults. Probably predation on birds by introduced *B. irregularis* on Guam is a retained primitive feeding pattern, whereas that species' diet of rodents on New Guinea and euryphagy by *B. dendrophila* throughout its range are correlated with local ecological factors. With few exceptions (e.g., a mouse-deer in *B. dendrophila*), prey/predator mass ratios are not large compared to other snakes. Morphological and ecological considerations suggest that, like *B. irregularis*, several other species of cat snakes could have catastrophic impact as introduced predators on island bird and bat faunas.

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INTRODUCTION

The Old World genus *Boiga* includes approximately 25 species of moderate to large, rear-fanged colubrids (Leviton 1970; Kroon 1973; Rasmussen 1979), often called cat or tree snakes because of their nocturnal, arboreal habits and vertical pupils. This report surveys published information on feeding in cat snakes, and analyzes additional data based on the examination of museum specimens. It addresses the nature of dietary and behavioral variation within and among 21 species of *Boiga*, and discusses ecological,

evolutionary, and conservation implications of that variation.

The feeding biology of cat snakes is of special interest for at least three reasons:

(1) *Boiga* is morphologically and ecologically diverse, and thus offers interesting material for broader evolutionary considerations. For example, although rear-fanged snakes play prominent roles in discussions of venom evolution (e.g., Smith and Bellairs 1947; Kardong 1979, 1980; Savitzky 1980), an understanding of that problem is hampered by a lack of information

on the feeding biology and phylogenetic relationships of informative taxa (Cadle 1983).

(2) Cat snakes might be important arboreal predators on vertebrates in many Old World tropical ecosystems, and three to five species of *Boiga* sometimes occur sympatrically (e.g., Taylor 1922a; Lim 1955; Lloyd et al. 1968; Kroon 1973; Inger and Colwell 1977). Autecological analyses provide data for subsequent community-level research, information that could not be obtained for snakes at a single site during a short-term study (Greene 1988a).

(3) Predation by *Boiga irregularis* was a key factor in the recent, precipitous decline of bird populations on the Pacific island of Guam, where that species was inadvertently introduced in the 1940s (Savidge 1984, 1987, 1988; Conry 1988; Fritts 1988). Island populations of fruit bats, already widely threatened by direct human persecution, might be at risk as well (Wiles 1988). Data on the natural diets of cat snakes could prove useful in managing this problem and preventing additional catastrophes.

METHODS

Stomach contents were examined through ventral slits in specimens in the Academy of Natural Sciences of Philadelphia (ANSP); American Museum of Natural History, New York (AMNH); California Academy of Sciences, San Francisco (CAS); Field Museum of Natural History, Chicago (FMNH); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museum of Southwestern Biology, University of New Mexico, Albuquerque (MSB); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); and National Museum of Natural History, Washington (USNM). I avoided especially soft, brittle, or otherwise fragile specimens; all others for each species were examined to preclude a bias for large prey caused by opening only snakes with externally palpable food items. My results also incorporate data on 10 New Guinea specimens of *Boiga irregularis* that contained prey (R. Shine, in litt.) in the Australian Museum (AM) and Queensland Museum (QM), and specific published information on feeding. I took care to account for redundancy among literature records and museum specimens (e.g., Schmidt 1927 and Pope 1935; Smith 1916 and 1930), and sometimes obtained information not mentioned previously.

Direction of ingestion, identity, and linear dimensions of prey items were recorded whenever possible. Intact prey items (or a reference specimen of comparable size) and the predators were weighed after blotting and draining them briefly on paper towels. Abbreviations refer to snout-vent length (SVL), total length (TL), maximum total length (MTL), and prey/predator mass ratio (MR). All bird or lizard eggs in a stomach were counted as one item, because they might represent a single location event and because sometimes the exact number of items was impossible to determine.

SPECIES ACCOUNTS

Boiga angulata (Peters 1861)

Philippine Islands, MTL 1.4 m (Leviton 1970). Four snakes contained five agamid lizards (1 *Calotes* sp., 3 *Draco* sp., $\bar{x}$ = 1.3/snake; Griffin 1910; CAS 154175, CAS-SU 24179; FMNH 61620). MRs for two *Draco* sp. in snakes with SVLs of 646 and 1,079 mm were 0.39 and 0.12, respectively. Two *Draco* sp. and an unidentified agamid were swallowed head-first.

Boiga blandingi (Hallowell 1857), Blanding's Tree Snake

Africa, MTL 2.7 m (Pitman 1974; Goodman 1985). Fifteen specimens contained at least 30 prey items ($\bar{x}$ = 2.0/snake): a 1.8 m TL snake contained 1 agamid lizard (*Agama agama*) and ca. 8 bats (*Eptesicus tenuipennis*, Vespertilionidae; *Tadarida* sp., Molossidae); 5 each contained 1 bat; 1 contained bats and 1 lizard; 1 contained a chameleonid lizard; 1 contained 4 birds; 1 contained a sunbird (*Nectarina famosa*); 4 each contained 1 bird, 2 swallowed head-first; and 1 contained 3 bats, swallowed tail-first, MRs = 0.03/each (Laurent 1956; Woodward 1960; Barry 1961; Cozens 1961; Dunger 1961; Menzies 1961; Pitman 1962; Hedges 1983; FMNH 179319–20; MCZ 54007). Three adults in one tree each contained young weaver birds, *Plesiositagra cucullatus*, and others contained fledgling birds and immature rats (Jones 1961).

Boiga ceylonensis (Günther 1858), Sri Lankan Cat Snake

India and Sri Lanka, MTL 1.6 m (Smith 1943). Forty-two prey items included 8 frogs (1 *Rana*

limnocharis, Ranidae; 5 *Philautus* sp., Rhacophoridae), 21 lizards (1 Gekkonidae; 2 *Calotes* sp., 3 *C. versicolor*, 1 *Charasia dorsalis*, 3 *Salea horsfieldi*, Agamidae), 3 birds (1 fledgling), and 2 mice (Wall 1919 [including snakes referred to as *B. nuchalis*], 1923, 1924; Hutton 1949; Taylor 1953; FMNH 131380, 167006). Two lizards were swallowed head-first.

***Boiga cyanea* (Dumeril and Bibron 1854),
Green Cat Snake**

India and Southeast Asia, MTL 2.3 m (Smith 1943). Seven snakes contained 1 snake (a female *B. cyanea*, 1,350 mm TL, in a 1,260 mm TL male) and 6 birds (1 sparrow [*Passer* sp., Passeridae], 1 probable wagtail [*Motacilla* sp., Motacillidae, in a snake of 821 mm SVL], 1 week-old domestic chick [*Gallus gallus*, Phasianidae]; Smith and Kloss 1915; Saint Girons 1972; Frith 1977; MCZ 58260). One bird had been swallowed head-first.

***Boiga cynodon* (Boie 1827),
Dog-toothed Cat Snake**

Southeast Asia and Indo-Australian Archipelago; MTL 2.8 m (Smith 1943; Saint Girons 1972; Kroon 1973; Tweedie 1983; FMNH 131809). Nineteen snakes contained 20 items ($\bar{x}$ = 1.05/snake), including 3 lizards (*Draco* sp., *D. volans*, Agamidae; *Gekko gecko*, Gekkonidae), 12 birds, 4 or more bird eggs, and 1 rodent (Flower 1899; Auffenberg 1980; ANSP 26421; CAS 8533, 125173; FMNH 53454–6, 71628, 131809, 131811, 150883, 158652–3, 168006, 183749). One lizard, 1 rodent, and 5 birds were swallowed head-first. A small snake (SVL = 360 mm) had eaten a *Draco* sp., and a juvenile (SVL = 640 mm) contained a relatively large bird (MR = 0.44). An intact bird's egg, maximum diameter 51 mm, was swallowed by a snake with head length of 52.2 mm.

***Boiga dendrophila* (Boie 1827),
Mangrove Snake**

Southeast Asia and nearby archipelagos, MTL 2.8 m (Burger 1975; Tweedie 1983). Fifty-four prey items in 52 snakes ($\bar{x}$ = 1.04/snake) included 1 frog, 15 lizards (9 scincids [2 *Lamprolepis smaragdinum*]; 2 lacertids, *Tachydromus sexlineatus*; 3 agamids [2 *Calotes* sp., 1 *C. cristatellus*];

1 varanid, *Varanus salvator*); 7 snakes (1 *B. cynodon*, 2 *Chrysopelea ornata*, 1 *Psammodynastes pulverulentus*, Colubridae; 1 *Calloselasma rhodostoma*, Viperidae); 17 mammals (2 bats [1 *Eonycteris spelea*, Pteropodidae], 1 mouse-deer [*Tragululus javanicus*, Tragulidae], 14 rodents [probably mostly Muridae, including *Rattus* sp.]); and 13 birds (Flower 1899; Smith 1916, 1930; Taylor 1922b; Brongersma 1934; Harrison 1962; Leviton 1970; Lim 1973; Minton and Dunson 1978; Smith 1985; ANSP 26417–8; CAS 12362–3, 15313; CAS-SU 28525–6; FMNH 53460, 53462, 53466, 68912, 71630, 96609, 120393, 131808, 150879, 158679, 178602, 230061).

Juvenile *Boiga dendrophila* eat mainly ectotherms (lizards and rarely snakes), whereas adults eat mainly birds and/or mammals (5/6 times vs. 25/34 items, respectively, using Brongersma's [1934] sample and museum records; P = 0.01, Fisher Exact Test). Sample sizes are insufficient for statistical comparisons, but I detect no evidence for major geographic variation in the diet of adults: frequencies of lizards, snakes, birds, and mammals, respectively, are 1, 1, 5, and 3 for Borneo; 5, 2, 2, and 5 for the Philippine Islands (all of the mammals were in Palawan mangrove snakes); 2, 1, 3, and 0 for Sulawesi; and 1, 3, 0, and 2 for mainland Asia. The largest snake containing a lizard and the smallest containing an endotherm had SVLs of 1,112 mm and 840 mm, respectively. Four lizards, 3 snakes, 3 birds, 4 rodents, and 1 adult mouse-deer were swallowed head-first, the latter by a 1.7 m TL snake. MRs for 2 lizards and a bird were 0.10–0.18 ($\bar{x}$ = 0.14).

***Boiga dightoni* (Boulenger 1894)**

India, MTL 1.3 m (Smith 1943). One adult (SVL = 915 mm) contained an agamid lizard, *Calotes versicolor*, swallowed head-first, MR = 0.24 (FMNH 217699 [Inger et al. 1984]).

***Boiga drapiezii* (Boie 1827),
White-spotted Cat Snake**

Southeast Asia, MTL 2.1 m (Tweedie 1954, 1983). Eight prey items included 5 lizards (1 Gekkonidae; 1 *Draco* sp., 1 *Gonocephalus* sp., Agamidae), 1 rhacophorid frog, and 2 birds (Lim 1956; FMNH 131804, 138594, 196805–6). Both agamids and the frog were swallowed head-first. MRs for the gecko and *Draco* were both 0.25.

Boiga forsteni (Dumeril and Bibron 1854)

Sri Lanka and India, MTL 2.3 m (de Silva 1980). Stomachs contained birds and a bat (Wall 1921).

Boiga gokool (Gray 1834),
Eastern Gamma Cat Snake

Asia and India, MTL 1.2 m (Smith 1943). Two snakes contained a mouse and an agamid lizard, the latter swallowed head-first (Wall 1910; MCZ 58261).

Boiga irregularis (Merrem 1790),
Brown Tree Snake

New Guinea, northern Australia, and nearby archipelagos; MTL 2.3 m (Fritts 1988). Fifty-nine snakes contained 65 items (1–3 per stomach, $\bar{x} = 1.10$), including 2 frogs (1 *Rana* sp., Ranidae), 19 lizards (1 agamid, *Gonocephalus modestus*; 10 scincids [2 *Emoia cyanura*, 3 *Lamprolepis smaragdinus*], 8 gekkonids [1 *Gehyra* sp., 2 *G. mutilata*, 1 *Gekko vittatus*]), 13 birds (1 passerine, 1 owl-nightjar [*Aegotheles bennettii*, Aegothelidae], 2 starlings [*Aplonis* sp., Sturnidae], 1 quail [*Coturnix chinensis*, Phasianidae]), and 30 mammals (1 marsupial bandicoot, Peramelidae; 1 bat; 1 shrew, *Crociodura* sp.; 17 rodents (5 juveniles, 1 adult *Rattus exulans*, 1 *R. rattus*, 1 *Mus musculus*, all murids; Rooij 1917; Kopstein 1926; Hediger 1933; Pendleton 1947; McDowell 1984; AM 4553, 11825, 12443, 12542, 14858, 86923, 87463, 87466; AMNH 40233, 42339, 42371, 59083, 62031–2, 65513, 73962, 85727–8, 85731, 95553, 95607, 101080, 101083; CAS 49910, 94027, 103388, 113600, 121224; FMNH 14076, 41980; QM 4381, 13.1280; USNM 6197, 61918, 61920, 159971, 195594, 213431, 215938, 215942, 215947, 216007, 216009, 237136, 237634). Stomachs with multiple prey included 1 with 2 *E. cyanura*, 1 with 2 *G. mutilata*, 1 with 2 young *Aplonis* sp., and 1 with 3 nestling rodents (apparently a single species). Three “bird” records consisted of 1 egg, several eggs, and 1 bird plus 2–5 eggs.

Forty-eight measurable individuals containing prey had SVLs of 292–1,710 mm. A 285 mm SVL specimen had an obvious umbilical scar, and six females containing enlarged ova or shelled oviductal eggs had SVLs of 840–1,305 mm. On

those bases, I divided snakes containing prey into “juveniles” (equal to or less than 750 mm SVL) and “adults” (greater than 750 mm SVL). Juveniles take significantly more ectothermic prey (snake, frogs, lizards) vs. endothermic prey (birds, mammals), whereas adults show the opposite bias (14:3 vs. 6:32, respectively; $P < 0.01$, χ^2 test). The largest snake containing a lizard was 1,000 mm SVL, the smallest containing an endotherm was 646 mm SVL, and the shift from emphasis on one prey type to the other occurs at ca. 800–900 mm SVL (Fig. 1). Larger snakes ate larger prey than did smaller snakes (Fig. 2). Prey/predator mass ratios ranged from 0.004–0.241 ($\bar{x} = 0.106$, $n = 13$), and the largest item was a 32 g starling (*Aplonis* sp.) in a 152 g *Boiga irregularis* from the Bismark Archipelago.

The 65 prey items are from throughout the species’ range except for Australia, where the diet of this species is under study by R. Shine. There is significant geographic variation in diet ($P < 0.01$, χ^2 test) if 38 records for endothermic prey are divided into those from mainland New Guinea vs. those from smaller islands (all others except Sulawesi, including the Solomon, Bismarck, and Molucca groups). Snakes from New Guinea ate mammals more frequently than they ate birds (19:3), in agreement with summaries of unspecified numbers of prey (Room 1974; Parker 1982) and general comments about diet on the tags of AMNH 74506 and 82334. The single diet record from Sulawesi, also a “large island,” was of a mammal. Snakes from “smaller islands” consumed birds and their eggs more frequently than they ate mammals (10:6).

Direction of ingestion was determined for 36 prey items. Twenty-eight were swallowed head-first, including 2 frogs, 8 lizards, 11 birds, 1 bat, 1 snake, and 5 rodents. Seven were swallowed tail-first, including 2 lizards, 1 bird, and 4 rodents. One lizard was swallowed bent doubled.

Savidge (1988) analyzed 494 prey items in 353 *Boiga irregularis* from an introduced population on Guam. As in natural populations, those snakes ate primarily lizards as juveniles and birds and/or mammals as adults. Her mean of 1.4 items/snake is higher than I observed, perhaps because she counted eggs as individual items in a stomach. Wiles (1988) reported three juvenile fruit bats in the stomach of a 2.5 m TL snake on Guam, and indirect evidence that these snakes were raiding bat roosts.

Boiga jaspidea (Dumeril and Bibron 1854),
Jasper Cat Snake

Southeast Asia, MTL 1.5 m (Taylor 1965; Tweedie 1983). Stomachs contained 1 agamid lizard (*Calotes* sp.), 1 bird, and 1 tree-mouse (*Chiropodomys gliroides*, Muridae) in a 1,213 mm TL snake (Lim 1956, 1967).

Boiga kraepelini Stejneger (1902)

East Asia and nearby islands, MTL 1.6 m (Kuntz 1963). Four snakes contained 2 agamid lizards (swallowed head-first), 2 birds, and 2 bird eggs, ready to hatch (Pope 1935; CAS 18891–2; FMNH 24986).

Boiga multifasciata (Blyth 1860),
Himalayan Cat Snake

Himalayan region, MTL 1.06 m (Smith 1943). One contained an agamid lizard, *Japalura variegata* (Wall 1909).

Boiga multomaculata (Boie 1827),
Large-spotted Cat Snake

East Asia, Java, Sumatra, and Borneo; MTL 1.2 m (Smith 1943). Stomachs contained 6 birds (1 *Motacilla* sp., Motacillidae) and 8 agamid lizards (*Calotes* sp., *C. versicolor*); three lizards (1 with MR = 0.58) and a bird were swallowed head-first (Wall 1926a, b; Schmidt 1927; Pope 1935; FMNH 26451, 105704, 178666; MSB 40769).

Boiga nigriceps (Günther 1863),
Dark-headed Cat Snake

South Asia and nearby archipelagos; MTL 1.7 m (Rooij 1917). One snake contained a bird, swallowed head-first (FMNH 128150).

Boiga ocellata Kroon (1973)

South Asia; MTL 1.7 m (Kroon 1973). Two adults contained a bird and a bird egg (FMNH 191998–9).

Boiga ochracea (Günther 1868),
Tawny Cat Snake

Asia, MTL 1.3 m (Smith 1943). Ten prey items included 8 agamid lizards (2 *Japalura variegata*,

3 *Calotes* sp.), 1 fledgling bird, and 1 mass of bird eggs; three of the agamids were swallowed head-first (Wall 1909, 1926a, as *B. hexagonatus*; CAS 12365, 95252).

Boiga pulverulenta (Fischer 1856),
Powdered Tree Snake

Africa, MTL 1.3 m (Pitman 1974). Ten snakes contained 13 prey items ($\bar{x}$ = 1.3/snake): 3 mice (2 juvenile *Praomys* sp., Muridae, in 1 snake), 2 agamid lizards, and 8 birds (Werner 1909; Pitman 1974; FMNH 4017, 59006–7; LACM 38688, 46328; MCZ 29354, 29357; USNM 223775). Two lizards and 6 birds were swallowed head-first; 2 snakes containing lizards were 330 and 850 mm SVL, whereas 5 containing birds were ca. 700–780 mm SVL. MRs were 0.12 for each lizard and 0.15 for each of 4 birds in 2 snakes ($\bar{x}$ = 1.4). One record of a bat in this species (Woodward 1960) is based on a misidentified *B. blandingi* (see above).

Boiga schultzei Taylor (1923)

Philippine Islands; MTL 1.4 m (Taylor 1923). A juvenile, SVL 310 mm, had swallowed 2 gekkonid lizards, *Gehyra mutilata*, head first (CAS 62153).

Boiga trigonata (Schneider in Bechstein 1802),
Gamma Cat Snake

Southern Asia, India, Sri Lanka; MTL 1.2 m (Smith 1943). “. . . the commonest contents were birds, chickens and eggs” (Lindberg 1932). Fourteen snakes contained 15 prey ($\bar{x}$ = 1.07 items/snake), including 11 lizards (*Acanthodactylus* sp., Lacertidae; at least 4 *Calotes* sp., 2 *C. versicolor*, Agamidae; 1 scincid; 1 set of 3 lizard eggs) and 3 birds (1 *Saxicoloides fulica*, Muscicapidae); two lizards and 1 bird were swallowed head-first (Wall 1907a, 1919, 1921; Minton 1966; Sharma and Vazirani 1977; CAS 13686; FMNH 131958, 166998, 171761). Ants and grasshoppers in the stomach of a small Indian specimen (Sunder Singh 1960) were probably remnants from the stomach contents of a prey lizard.

DISCUSSION

INDIVIDUAL AND GEOGRAPHIC DIETARY VARIATION.—Intraspecific variation in snake diets can include intra- and interindividual, on-

togenetic, seasonal, and geographic components (Arnold 1977; Greene 1984; Seib 1985; Mushinsky 1987; Macias Garcia and Drummond 1988; Savidge 1988). At one extreme, *Thamnophis elegans* (Colubridae) shows extensive geographic variation, and litter mates have genetic predispositions for alternative prey types (Arnold 1977); conversely, the diet of *Micrurus fulvius* (Elapidae) varies only slightly at all sizes and throughout the year over a large geographic range (Greene 1984).

In studies of museum specimens, evidence for intraindividual dietary variation comes from multiple prey types in single stomachs, as in a *Boiga ceylonensis* that contained a bird and two mice, and two *B. blandingi* that each contained bats and a lizard. All such records for *B. angulata*, *B. cynodon*, *B. dendrophila*, *B. irregularis*, *B. kraepelini*, *B. ochracea*, *B. pulverulenta*, *B. schultzei*, and *B. trigonata* apparently are multiples of one prey species, as are several records for *B. blandingi*. Of 353 *B. irregularis* on Guam that contained prey, 67 had more than one item of the same "prey type" (e.g., lizards and/or lizard eggs, birds and/or bird eggs); 14 had lizards and birds or mammals, as expected for small adults; and only five (<6% of stomachs with multiple items) contained birds and/or their eggs and mammals (Savidge 1988). These data suggest that individual cat snakes rarely eat birds and mammals, at least within a short time period. Some species, however, often consume more than one of the same prey type (and even same prey species), and perhaps this is especially true for *B. blandingi*. Surely the clumped distribution of roosting bats and nestling birds facilitates multiple ingestion.

There is significant geographic dietary variation in *Boiga irregularis* within its natural range, and microgeographic variation in predation on rodents vs. birds in urban vs. forest habitats by introduced snakes on Guam (data from Savidge [1988, table 1], χ^2 test, $P < 0.01$). The data for other species of *Boiga* are inadequate to distinguish geographic from individual and ontogenetic variation.

Perhaps diet is plastic at some localities, or throughout all or part of the range of some species of *Boiga*. If so, interspecific and geographic patterns could result from individual responses to local prey characteristics and/or availability, rather than from dietary evolution. The infre-

quent occurrence of multiple prey types in individual stomachs of several species of *Boiga* is consistent with stable prey preferences, whereas there evidently has been a rapid local response by *B. irregularis* to shifting prey densities on Guam (Savidge 1988, and see above; Greenwell et al. [1984] described a possible example involving *Thamnophis sirtalis* and birds on an island, and Chiszar [1989] discussed the behavioral basis for prey switching in *B. irregularis*). Genetic differentiation and phenotypic plasticity are not mutually exclusive, in that response to local conditions could override genealogically constrained prey preferences, and a thorough assessment of these possibilities for cat snakes will require studies of the ontogeny and control of feeding behavior in several populations.

PREY/PREDATOR SIZE RELATIONSHIPS AND ONTOGENETIC VARIATION.—As in other snakes (Greene 1984; Seib 1984, 1985), larger individuals of *Boiga* eat larger prey, and also continue to eat relatively small prey (Fig. 2). Most MRs for eight species of *Boiga* are not especially large compared with those of other snakes (0.004–0.58, $\bar{x} = 0.16$, $n = 32$; cf. Voris and Moffett 1981; Greene 1983, 1984, 1989; Seib 1984, 1985; Jayne et al. 1988). However, a 1.7 m *B. dendrophila* would weigh no more than 1 kg (pers. obs.) and lesser mouse-deer weigh 0.7–2.0 kg (Lekagul and McNeely 1977), so the latter is a relatively large item. A bandicoot in *B. irregularis* and prey snakes longer than the *B. cyanea* and *B. dendrophila* that contained them (Smith and Kloss 1915; Smith 1916) likewise were surely relatively heavy; a captive *B. irregularis* consumed a domestic rodent with MR = 0.60 (Chiszar 1989). Records for *B. irregularis* and *B. pulverulenta* demonstrate that a cat snake can ingest at least a third of its mass if it eats more than one item in a nest or roost.

Data from its natural range and the introduced Guam population agree that *Boiga irregularis* changes from eating mainly lizards to eating mainly birds and/or mammals at a SVL of ca. 80–100 cm. Similar shifts evidently occur in *B. dendrophila* and *B. pulverulenta*, and seem likely for other large species of *Boiga* (Fig. 1). Perhaps that pattern reflects simply an ability of larger snakes to swallow larger prey, since slopes and intercepts for endothermic vs. ectothermic prey are similar (analysis of covariance for data in Fig. 2, $P > 0.05$). However, large snakes eat endo-

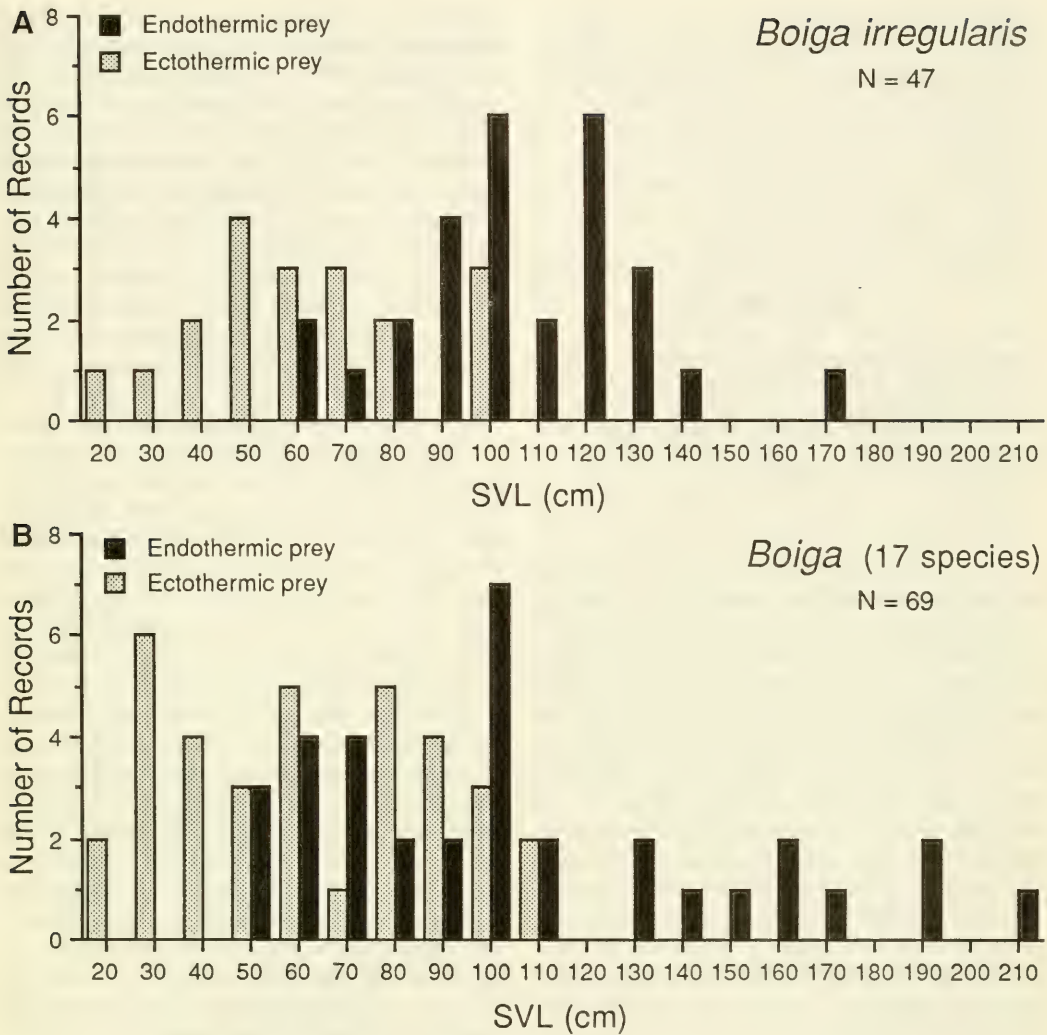


FIGURE 1. Records for ectothermic and endothermic prey with respect to predator snout-vent length in cat snakes, genus *Boiga*. For this comparison, multiple items of one prey type in a single stomach were counted once.

therms that are smaller than the ectotherms taken by smaller snakes (Fig. 2), implying that larger snakes fail to encounter small ectotherms or have undergone a real change in prey preference.

FEEDING BEHAVIOR.—Most *Boiga* prey mainly on diurnal, arboreal lizards (especially agamids of the genus *Calotes*) and diurnal birds. Studies on free-living and captive *B. irregularis* suggest that these nocturnal hunters must search for rather than ambush inactive prey (Fritts et al. 1987; Savidge 1988; Chiszar 1989; Chiszar et al. 1985, 1988). Jones (*in* Pitman 1958) saw three *B. blan-*

dingi “pushing their heads into one nest after the other and taking the young [weaver birds]. . .” However, a *B. dendrophila* constricting an *Eonycteris spelea* in a tree after dark probably ambushed the bat while it was feeding on or approaching fruit, as that species typically roosts in caves (Harrison 1962).

Some *Boiga cynodon*, *B. dendrophila*, and *B. trigonata* constrict prey with the tail as well as hold and presumably envenomate an animal with their teeth (Wall 1907b, 1921; Barach 1952; Murphy 1977; however, Lim et al. [1960] stated

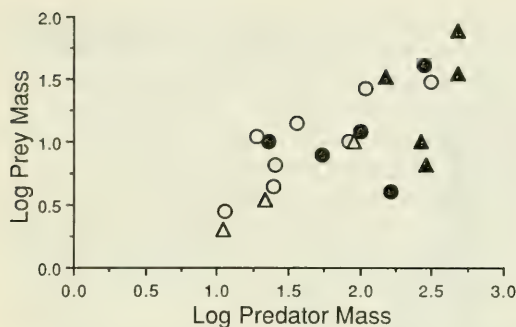


FIGURE 2. Relationship between log predator mass and log prey mass for *Boiga irregularis* (triangles, $n = 8$) and eight other species of *Boiga* (circles, $n = 13$). Hollow symbols indicate ectothermic prey; solid symbols indicate endothermic prey. For this comparison, multiple items of one prey type in a single stomach were counted once.

that *B. cynodon* does not constrict prey). *Boiga multomaculata* constricts lizards, but the precise method is unknown (Campden-Main 1970). *Boiga blandingi* and *B. ceylonensis* do not constrict prey, whereas *B. forsteni* and *B. irregularis* vary in this regard (Groves 1973; Murphy 1977; de Silva 1980; Parker 1982; Shine and Schwaner 1985; Fritts 1988). Young (1983) observed that *B. blandingi* controlled prey with loops of the body, but did not constrict; that *B. cyanea* overpowered live mice with constriction "in a manner similar to that of a rat snake or a king snake"; that *B. cynodon* did not constrict, but controlled live prey with loose coils of the anterior body; and that *B. dendrophila* was "an efficient and powerful constrictor . . . upon warm blooded prey, but it rarely employed this behavior . . . on snakes." Captive *B. irregularis* swallow small prey immediately and apply constricting coils to relatively heavy prey (Chiszar 1989).

Additional inter- and intraspecific comparisons will be required to elucidate the variation in and evolution of prey-immobilization behavior in *Boiga*. Constriction with the tail is rare among snakes (Murphy 1977; Greene 1977) and absent in the outgroup to *Boiga* (see below), suggesting three possibilities: (1) It is a derived state for *Boiga*, either as yet unobserved or secondarily lost in most species; (2) some other derived attribute of *Boiga* (e.g., arboreality, long tails, multiple constriction of nestlings) favors this type of constriction and it arose repeatedly in the genus; or (3) constriction with the tail is a derived at-

tribute for a monophyletic subset of *Boiga*, a behavioral synapomorphy for those species.

The venom of *B. blandingi* is neurotoxic and can kill a large rodent or a small monkey in less than an hour (Wakeman 1966; Groves 1973; Levinson et al. 1976), and at least some other species have venom that is slightly or moderately toxic to humans (e.g., Deraniyagala 1955; Whitaker 1970; Burger 1975; Minton and Dunson 1978; Cox 1988; Fritts 1988). A captive adult *B. dendrophila* (TL ca. 1.8 m) had difficulty subduing and swallowing adult laboratory rats (Barach 1952), but those animals can be powerful opponents for captive snakes (pers. obs.).

Head-first prey ingestion is the norm in nature for *Boiga irregularis* (28/36 items, $P < 0.01$, χ^2 test), as it is for many other snakes (e.g., Greene 1976, 1983, 1984, 1989; Ananjeva and Orlov 1982; Voris and Voris 1983; Seib 1984, 1985). Of 61 cases for which direction of ingestion was determined for 16 other species of *Boiga*, 58 were swallowed head-first; 3 bats were eaten tail-first.

EVOLUTIONARY IMPLICATIONS.—An evolutionary consideration of feeding necessitates the categorization of dietary variation into alternative states and the identification of appropriate outgroups, so that the distribution of states among populations, taxa, and outgroups can be used to specify transformations during the history of that clade (see Arnold 1981; Kluge 1987; Losos and Greene 1988). A phylogenetic consideration of feeding in *Boiga* and its relatives, although based on incomplete data, has implications that justify the following preliminary analysis.

The precise relationships of *Boiga* to other colubrids are unknown; Rasmussen (1979, 1985) placed it with the African genera *Crotaphopeltis*, *Dipsadoboa*, and *Telescopus*, so these are used here as a collective outgroup. Species of *Crotaphopeltis* are terrestrial and feed on toads. Species of *Dipsadoboa* are arboreal and feed on frogs and lizards. The Eurasian species of *Telescopus* evidently are terrestrial, whereas the African *T. dhara* and *T. semiannulatus* are arboreal; all eat lizards and occasionally birds and bats. Species in all three genera are nocturnal and reach MTLs of ca. 1 m (Corkhill 1932; Pitman 1974; Broadley 1983).

Most species of *Boiga* are small to moderately long snakes that eat lizards throughout their lives, or large snakes that eat lizards as juveniles and endotherms as adults. Division of the second of

those qualitative groups into four subgroups yields a total of five dietary character states:

Diet-1 consists primarily of lizards throughout life, with an occasional bird or mammal. *Boiga ceylonensis* possesses this diet, as do perhaps *B. angulata*, *B. dightoni*, *B. gokool*, and *B. ocracea*. These species have MTLs of 1.2–1.6 m.

Diet-2 consists of lizards in juveniles, mainly of birds in adults. *Boiga cynodon*, some populations of *B. irregularis*, and *B. multomaculata* exhibit this diet, as do perhaps *B. drapiezii*, *B. forsteni*, *B. kraepeleni*, *B. nigriceps*, *B. ocellata*, and *B. trigonata*. These species have MTLs of 1.2–2.8 m.

Diet-3 consists of lizards in juveniles, mainly of rodents in adults. Only *Boiga irregularis* (MTL = 2.3 m) on New Guinea exhibits this state.

Diet-4 consists of lizards in juveniles, mainly of mammals and birds in adults. *Boiga blandingi* and perhaps *B. cyanea*, *B. jaspidea*, and *B. pulverulentus* exhibit this state, and have MTLs of 1.3–2.8 m. However, sample sizes are quite small except for the first species, and in no case can the possibility of geographic variation for diet-2 and diet-3 be excluded. Also, bats are probably functionally equivalent to birds in shape and arboreal roosting behavior (Cundall and Greene, unpubl.; many other snakes that eat bats also eat birds, Schaetti 1984), so that *B. blandingi* perhaps should be assigned diet-2.

Diet-5 consists of lizards in juveniles, mainly of snakes, birds, and mammals in adults. Stomach contents and observations on captives (Young 1983) suggest that *Boiga dendrophila* is more euryphagous than other species in the genus.

Ingroup and outgroup comparisons indicate that *Boiga* is primitively nocturnal and perhaps derivatively arboreal. Diet-1 and relatively small MTL are found in a few species and in the outgroup, but lacking knowledge of intrageneric relationships, we cannot determine if their presence in *Boiga* is primitive or a reversal. Diet-2 and large size are widespread in species of *Boiga* and absent in the outgroup (with the possible exception of diet-2 in some *Telescopus*), but we cannot be sure if those characteristics are derived for the genus or within *Boiga*, perhaps more than once.

Diet-2 is probably primitive for adult *Boiga irregularis*, based on widespread occurrence in the genus, suggesting that diet-3 is derived within that species, but the reasons for intraspecific geo-

graphic variation are not known. Birds are rarely eaten by *B. irregularis* in New Guinea, although the island has a rich avifauna (Beehler et al. 1986). Several species of New Guinea birds exhibit nesting attributes that are possibly antipredator specializations (J. M. Diamond, University of California, Los Angeles, in litt.), but perhaps so do birds on other islands and the mainland that are commonly eaten by other species of *Boiga*. A niche shift in response to competitive pressure seems unlikely, because no other New Guinea snakes are known to feed heavily on birds (McDowell 1969, 1972, 1975, 1984; Shine 1980a; Parker 1982; Malnate and Underwood 1988). Perhaps New Guinea arboreal rodents are so much more diverse and numerous than on nearby archipelagos (Laurie and Hill 1954; Menzies and Dennis 1979) that they provide "better" food per unit effort or are simply encountered more often than birds.

Based on ingroup and outgroup comparisons, diet-4 and diet-5 are probably derived within *Boiga*. Euryphagy evidently reaches a maximum for the genus in *B. dendrophila* and is correlated with a derived preference for riparian habitats (Taylor 1965; Frith 1977; Minton and Dunson 1978; Dring 1979; Cranbrook and Furtado 1988; this proclivity is not reported for other species of *Boiga* or the outgroup genera). Some theoretical foraging models predict that habitat specialization results in broader diets and use of suboptimal prey (e.g., MacArthur and Pianka 1966; Krebs et al. 1983). The relevance of those models for cat snakes could be explored with captive animals, in part, by testing the presumption that alternative prey types vary in profitability (see Godley 1980).

My findings on feeding biology in *Boiga* underscore some cautionary lessons with regard to the evolution of rear-fanged snakes:

(1) Ontogenetic and/or geographic variation can be sufficiently large that a proportional representation of overall diet for a species will obscure functional, biogeographic, and phylogenetic correlates: the overall sample for *Boiga irregularis* from throughout its natural range consists of approximately 32% lizards, 21% birds, and 44% mammals, but most individuals feed *entirely* on lizards as juveniles and on either mainly rodents or mainly birds as adults.

(2) The preceding analysis assumes that diets really are attributes of populations and taxa, and

that they have evolved conservatively (i.e., with minimal homoplasy). High rates of reversals and convergence can only be detected by detailed phylogenetic analysis, so there is as yet no basis for postulating this alternative for *Boiga*. The other possibility, that individual dietary plasticity accounts fully for geographic and systematic patterns, is discussed above (see INDIVIDUAL AND GEOGRAPHIC DIETARY VARIATION).

(3) There is no evidence that the venom apparatus of *Boiga* is functionally associated with feeding on prey that are especially heavy or otherwise costly, although rare ingestion of large prey remains a possibility (see *B. dendrophila*, above, and Greene 1986a).

(4) Rear fangs arose at the level of *Boiga* or, more likely, a more inclusive group (Rasmussen 1979, 1985). Whatever the ecological role of venom injection (if any) in extant cat snakes, its possible adaptive origin (if any) in the clade containing *Boiga* cannot be identified until additional information on suprageneric relationships and natural history are available (see Cadle 1983; Greene 1986a; Schaefer and Lauder 1986). To the extent those limitations apply to other clades, conclusions about the adaptive significance of rear-fanged dentition are premature.

ECOMORPHOLOGICAL SUITES AND CONVERGENT ANALOGUES.—Qualitative ecomorphological analogs have been identified among certain geographically and phylogenetically distant snakes (e.g., Shine 1980a, b, c; Henderson and Binder 1980), and suggestive parallels can be drawn between species of *Boiga* and certain other taxa. Some resemblance to Afro-Asian species of *Telescopus* might be either convergent or homologous (Rasmussen 1979, 1985); the two genera are largely allopatric. Rear-fanged colubrids of the Malagasy genus *Lycodryas* (Raxworthy 1988) and neotropical genus *Imantodes* (especially the *I. cenchoa* species group, Myers 1982) are arboreal, nocturnal, and resemble small species of *Boiga* in general body form (e.g., large head and eyes, slender neck) and diet. The New World, rear-fanged genus *Trimorphodon* is said to be related to *Boiga* (Dowling et al. 1983) or to several genera of New World colubrids (Minton and Salanito 1972; Cadle 1988; R. Lawson, CAS, pers. comm.). Both species of *Trimorphodon* are arboreal, nocturnal, and feed largely on sleeping, diurnal iguanid lizards; only certain populations of *T. biscutatus* occasionally include birds and

bats in the diet (Greene, unpubl. data). A non-venomous, diurnal neotropical colubrid, *Pseustes poecilonotus*, resembles *B. dendrophila* in size, diet, and defensive behavior; however, even juvenile *P. poecilonotus* eat small birds (Greene 1979, and unpubl. data). I detect no particular convergent resemblance, beyond arboreality, irascibility (Greene 1988b), and nocturnality, between *Boiga* and Australian elapids of the genus *Hoplocephalus* (Shine 1983).

CAT SNAKES AS INTRODUCED PREDATORS.—This study provides potentially useful insights with regard to the threat that introduced cat snakes pose for island prey faunas:

(1) Heavy predation on birds by *Boiga irregularis* on Guam probably reflects the primitive diet for this species (see above), rather than a feeding shift in response to special local conditions. It is not surprising that this snake makes heavy inroads on island bird populations, especially if acceptable alternative prey (e.g., rodents, see above) are unavailable or rare, and/or if the native avifauna has evolved behavioral and demographic attributes in the absence of predators (see Jackson [1974] for a bird with behavioral defenses against nest predation by snakes). The effects of an introduced snake on native island prey populations might be all the more rapid in the absence of natural predators on snakes (Greene 1988a).

(2) Neonate *Boiga irregularis* are evidently too small to eat endothermic prey, and starvation of juveniles is probably a major source of natural mortality in some snake populations (e.g., Fitch 1949). Potential control measures for introduced *Boiga* might include manipulating the availability or characteristics (e.g., artificial toxicity) of lizard prey.

(3) *Boiga irregularis* is a moderately large snake with a venom delivery system and constricting behavior that could permit it to subdue a wide range of prey sizes and types. Like several other species of *Boiga*, it possesses a relatively wide skull and long dentaries (Marx and Rabb 1972), derived characteristics that are likely associated with increased gape (Rasmussen 1979; Arnold 1983), thereby facilitating a diet of birds, eggs, and bats (Cundall and Greene, unpubl. data). Although not so highly specialized as to be unable to forage on the ground, evidently all species of *Boiga* climb well and are nocturnal.

Each of the above attributes of cat snakes might

enhance their ability to feed on sleeping diurnal birds and their eggs, or on roosting and foraging bats. For those reasons and/or because of known predation on birds and bats, all moderate to large *Boiga* are potentially catastrophic invaders of isolated island faunas. Species for special concern include *B. blandingi*, *B. cyanea*, *B. cynodon*, *B. dendrophila*, *B. drapezii*, *B. forsteni*, *B. irregularis*, *B. jaspidea*, *B. kraepelini*, *B. nigriceps*, *B. ocellata*, *B. pulverulenta*, *B. schultzei*, and *B. trigonata*. There is a clear potential for additional introductions: recently individual *B. irregularis* have reached several Pacific islands (Fritts 1988), at least one *B. dendrophila* landed on Taiwan in a shipment of lumber (A. H. T. Yu, pers. comm.), and several species of large *Boiga* are commonly available in the pet trade (pers. obs.).

EPILOGUE

I have never seen a *Boiga* in the field, and this research was made possible by the efforts of numerous collectors, curators, authors of anecdotes, and sponsors of natural history publications. Few of those individuals intended their specimens for studies on the evolution of feeding, and even fewer imagined that their labors would have implications for an urgent conservation problem. Nevertheless, starting from scratch to learn something comparable about the broader context for avian predation by introduced cat snakes on Guam would have required many years of work. Therein surely lie some lessons (see also Greene 1986b; Greene and Losos 1988).

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NEW SPECIES AND TAXONOMIC NOTES ON MEXICAN AND
CENTRAL AMERICAN MELASTOMATACEAE

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ABSTRACT: Descriptions, diagnostic illustrations, and discussions are presented for four new species of *Miconia*: *M. grayumii* from Costa Rica and Nicaragua; *M. ibarrae* from Mexico; *M. iteophylla* and *M. peltata* from Panamá. A reappraisal of the floral morphology of *Leandra consimilis* necessitates its transfer to *Miconia* and the adoption of a new name, *M. ligulata*. A chromosome number of $n = 11$ is reported for *Pilocosta oerstedii* subsp. *campanensis* for the first time. To reflect the uniqueness and relationships of subsp. *campanensis* it is elevated to specific status based on a reconsideration of morphological, chromosomal, and ecogeographic attributes.

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INTRODUCTION

Recent field work in Central America has generated a rich reservoir of specimens upon which to base a treatment of the Melastomataceae for Flora Mesoamericana. In the course of studying this material I continue to detect many new taxa, significant range extensions, nomenclatural problems in need of adjustment, and other information that enhances our understanding of previously described taxa. This paper records some of these discoveries and observations to make the names available for use in other regional checklists and floristic treatments of the family.

Miconia grayumii Almeda, sp. nov.

(Fig. 1)

TYPE.—COSTA RICA. Heredia: Finca La Selva, Field Station of the Organization for Tropical Studies on the Río Puerto Viejo E of its junction with the Río Sarapiquí, elev. ca. 100

m, 22 Oct. 1982, McDowell 576 (holotype: CAS!; isotype: DUKE).

Frutex vel arbuscula 1–5 m. Ramuli obscure quadrangulati demum teretes sicut petioli foliorum subtus venae primariae inflorescentiaque modice granuloso-furfuracei. Petioli (2–)6–21 mm longi; lamina 5.5–12.7 × 1.2–4.3 cm anguste elliptica apice anguste gradatimque acuminato basi late acuta vel obtusa, 3-plinervata, membranacea et undulato-denticulata vel integra. Inflorescentia 2.5–5 cm longa multiflora; flores 5-meri, pedicellis (ad anthesim) 2–2.5 mm longis, bracteolis 0.5 × 0.25 mm persistentibus. Hypanthium (ad torum) 1 mm longum sparsiuscule caduceque granuloso-furfuraceum; lobis interioribus 0.25 × 0.5 late deltoideis, dentibus exterioribus 0.25–0.5 mm eminentibus. Petala 1.5–2 × 0.5 mm obovato-oblonga intus minute papillosa extus glabra. Stamina isomorphica glabra; filamenta 1–1.5 mm longa; antherarum thecae 0.5–0.75 × 0.25 mm anguste oblongae, poro paulo dorsaliter inclinato; connectivum nec prolongatum nec appendiculatum. Stylus 2.5–3 mm glaber; ovarium 5-loculare et $\frac{3}{4}$ inferum glabro.

Shrub or small trees 1–5 m tall. Older cauline internodes subquadrate to terete, sparsely to moderately ferruginous scurfy-pulverulent to glabrate. Distal branchlets, petioles, elevated pri-

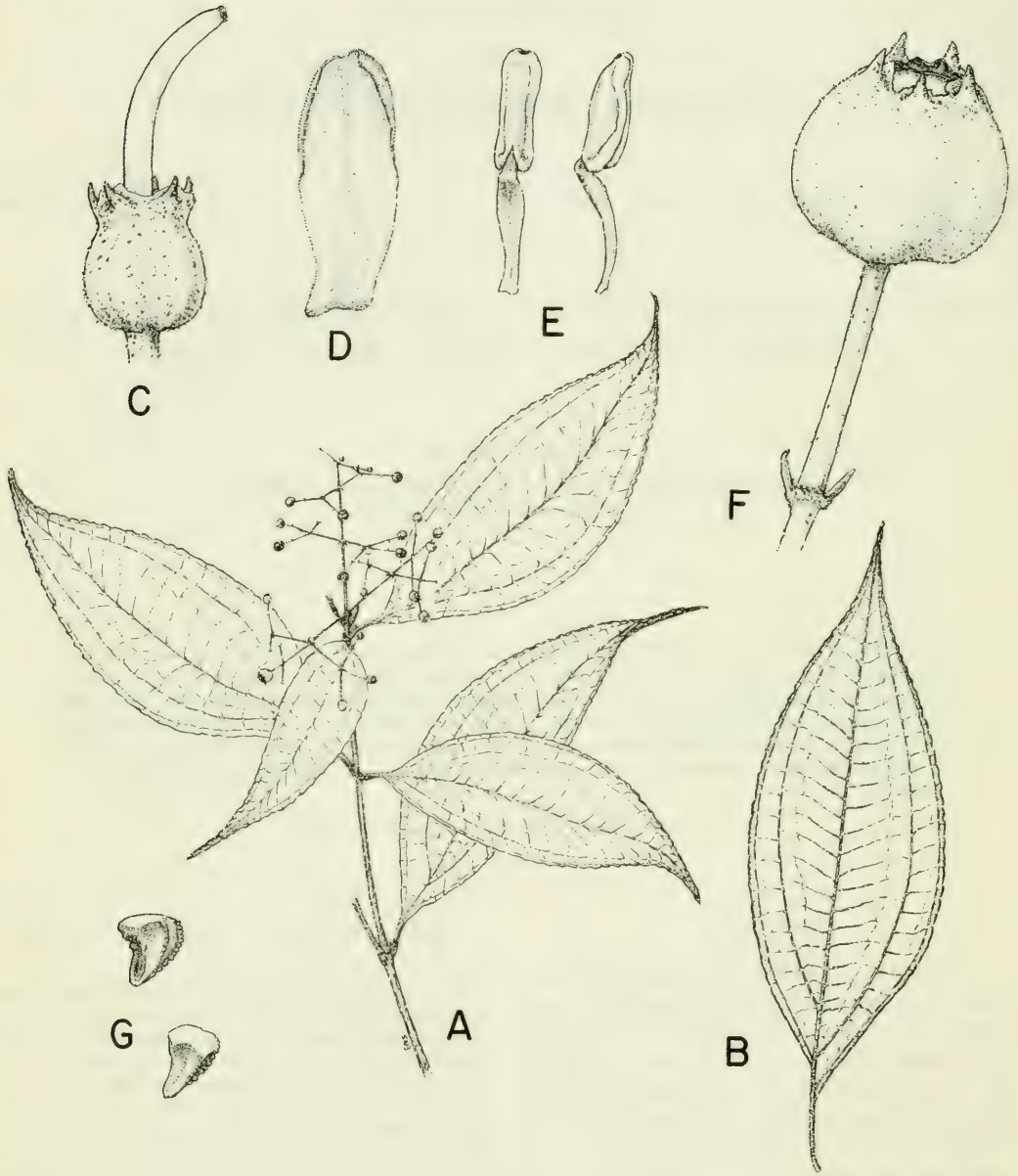


FIGURE 1. *Miconia grayumii* Almeda. A, habit, $\times$ ca. $\frac{2}{3}$; B, representative leaf (lower surface), $\times$ 1; C, flower (at anthesis) with all petals and stamens removed, $\times$ 15; D, petal (adaxial surface), $\times$ ca. 22; E, stamens, dorsal view (left) and lateral view (right), $\times$ 30; F, mature berry, $\times$ ca. 5; G, seeds, $\times$ ca. 15. (A from *Folsom* 8914; B from *Smith* 152; C–F from the holotype; G from *Hammel* 12011.)

mary leaf veins below, and inflorescences moderately scurfy-pulverulent. Leaves of a pair somewhat unequal in size; petioles (2)–6–21 mm long; blades membranaceous, 5.5–12.7 cm long and 1.2–4.3 cm wide, narrowly elliptic, apex attenuate to gradually acuminate, base broadly

acute to obtuse and typically inaequilateral but not decurrent on the petiole, margin undulate-denticulate to entire, 3-plinerved, the innermost pair of elevated primaries diverging from the median nerve in opposite or irregularly alternate fashion at successive points above the blade base,

the transverse secondaries prominulous and spaced 3–5 mm apart at the widest portion of the blade, glabrous above at maturity, sparingly scurfy-pulverulent and/or obscurely glandular-pulverulent to glabrate below. Inflorescence a paniculiform dichasium 2.5–5 cm long divaricately branched from the base, terminal but sometimes becoming pseudolateral because of axillary bud elongation; bracts of rachis nodes persistent, lance-triangular, 0.5–3 mm long, 0.25 mm wide, glabrous above, sparsely scurfy-pulverulent to glabrate below; bracteoles sessile and persistent, paired and fused into a short inconspicuous nodal collar or elevated interpetiolar ridge, lance-triangular to subulate, 0.5 mm long, 0.25 mm wide, glabrous above and sparingly scurfy-pulverulent to glabrous below, margin entire. Pedicels 2–2.5 mm long, sparingly and deciduously scurfy-pulverulent to glabrate. Hypanthium (at anthesis) globose, 1 mm long to the torus, sparsely and deciduously scurfy-pulverulent. Calyx lobes 5, rounded-deltoid, hyaline and glabrous, 0.25 mm long, ca. 0.5 mm wide basally between sinuses, the margins entire; exterior calyx teeth 5, subulate, 0.25–0.5 mm long, exceeding and obscuring the lobes, essentially glabrous throughout; torus glabrous adaxially. Petals 5, obscurely papillose adaxially, otherwise glabrous, white, obovate-oblong, rounded apically, 1.5–2 mm long, 0.5 mm wide distally. Stamens 10, isomorphic; filaments glabrous, complanate, 1–1.5 mm long; anthers 0.5–0.75 mm long, 0.25 mm wide, yellow, oblong, rounded to truncate at the apex with a retuse to somewhat dorsally inclined terminal pore; connective thickened dorsally but not prolonged or appendaged at the filament insertion. Ovary (at anthesis) ca. $\frac{3}{4}$ inferior, 5-celled, globose, glabrous apically. Style erect and conspicuously curved distally, glabrous, 2.5–3 mm long; stigma punctiform to truncate. Berry blue-black or purple at maturity, globose, 3–5 mm long and 3–5 mm in diameter. Seeds angulate-pyramidate, 0.5–1 mm long, beige, smooth with obscure but distinct verruculose angles on the convex face.

PHENOLOGY.—Flowering and fruiting occur sporadically from February through November.

DISTRIBUTION.—Rain forests and stream banks in the Caribbean lowlands of Costa Rica and Nicaragua at 40–180 m.

ADDITIONAL SPECIMENS EXAMINED.—COSTA RICA. Heredia: Finca La Selva, OTS Field Station on Río Puerto Viejo,

trail at perimeter of successional plots, 13 Feb. 1981, *Folsom 8914* (CAS); Finca La Selva, OTS Field Station, West Boundary, 800–1,200 m line, 19 Feb. 1981, *Folsom 9041* (CAS); W of San Jose on Río Sarapiquí, across Río Sardinal at edge of Lomas Sardinal, 4 Feb. 1983, *Garwood et al. 1070* (BM); Finca La Selva, Loop Trail, near SW Trail, 15 Jul. 1979, *Grayum 1834* (CAS); Finca La Selva, East Boundary Trail, 2,300 m line, 19 Jul. 1979, *Grayum & Sperry 1854* (CAS); Finca La Selva, forested knoll E of Boundary Trail on way to Q. Arboleda swamp, 14 Mar. 1980, *Hammel 8076* (CAS); Finca La Selva, bank along Río Puerto Viejo, 550 S $\times$ 1,500 E m grid, 23 Jun. 1980, *Hammel 9103* (CAS); Finca La Selva, near Loop Trail, 100 m S, 28 Aug. 1980, *Hammel 9603* (CAS); Finca La Selva, on ridge in plot III, 4 May 1982, *Hammel 12011* (CAS); Finca La Selva, West Boundary, 1,200 m S, 28 May 1982, *Hammel 12576* (CAS); Finca La Selva, El Sura Trail, 1,200 m line, 25 Sep. 1982, *McDowell 199* (CAS); Finca La Selva, around 1,850 m E, 1,950 m S, 1 Sep. 1981, *Smith 152* (CAS). Limón: Cerro Coronel, E of Río Zapote, ca. 1.5 km from Río Colorado, 10°40'N, 83°40'W, 13 Mar. 1987, *Stevens et al. 24795* (CAS). NICARAGUA. Zelaya: Nueva Guinea, Colonia Yolaina, 13 Aug. 1982, *Araguistain 3069* (CAS); Caño Costa Riquita, 1.8 km SW of Colonia Naciones Unidas, 11°43'N, 84°18'W, 6–7 Nov. 1977, *Stevens 4971* (CAS).

The first collections of *Miconia grayumii*, made just over a decade ago, were initially referred to *M. brenesii* Standley because of similarities in foliar morphology, indument type, and the divaricately branched dichasia. Critical study of the improved material now available necessitates the recognition of two species based on consistent morphological and ecological differences. All of the perceived differences between *M. grayumii* and *M. brenesii* involve details of the flowers and fruits. The latter has broadly deltoid calyx teeth that do not greatly exceed or obscure the calyx lobes, petals that are smooth on both surfaces, and anthers that are cuneate and broadest distally with flaring dorsally inclined pores. This broad pore and its thick connective that is prolonged for a short distance (0.25 mm) below the thecae give the anthers of *M. brenesii* an unusual dorsally arcuate conformation when dry. Some of the most readily observed differences between *M. grayumii* and *M. brenesii* involve stylar and seed characters. In *M. brenesii* the straight style is terminated by a capitellate stigma and its seeds, although pyramidate like *M. grayumii*, have completely smooth polished angles. There are also pronounced ecogeographic differences between these two species. In Costa Rica, *M. brenesii* is largely confined to a more westerly distribution at higher elevations (900–1,600 m) whereas *M. grayumii* occurs in the eastern lowlands (40–180 m) that extend northward to Nicaragua.

Despite the many vegetative similarities between *M. brenesii* and *M. grayumii*, the latter appears to be closest to *M. ligulata* Almeda (also discussed below). Petal, stamen, and seed morphology are identical in these two species. However, in *M. ligulata* the indument consists of pinoid hairs, the leaves are larger (12–28 × 4–10 cm) and decurrent on the petiole, the torus is puberulent adaxially, the petals are glabrous throughout, and the style is straight.

This species is named for Michael Grayum who first collected this species at the La Selva Field Station in 1979. His subsequent field work in many other areas of Costa Rica has added numerous interesting plants to the flora of the region.

***Miconia ibarrae* Almeda, sp. nov.**

(Fig. 2)

TYPE.—MEXICO, Veracruz: road to Lázaro Cárdenas, 4 km W of Estación de Biología Tropical Los Tuxtlas, 95°04' and 95°09'W, 18°36'N, municipio San Andrés Tuxtla, elev. 400 m, 3 Jun. 1986, *Sinica* 738 (holotype: CAS!; isotype: MEXU).

Arbor parva 4–9 m. Ramuli quadrangulati demum teretes sicut foliorum subtus venae primariae inflorescentia hypanthiaque modice vel sparse stellulato-furfuracei demum glabrati. Petioli 0.8–2.1 cm longi; lamina 5–11.5 × 2.5–4.1 cm elliptica vel elliptico-lanceolata apice acuminata basi acuta vel obtusa, 3(–5)-plinervata, membranacea et undulato-denticulata. Panicula 5–10 cm longa multiflora; flores 5-meri, pedicellis (ad anthesim) 0.5 mm longis, bracteolis 0.25–0.5 × 0.25 mm persistentibus. Hypanthium (ad torum) 2–2.5 mm longum; calyx 0.5 mm longus truncatus vel vix undulatus, dentibus exterioribus ca. 0.25 mm eminentibus. Petala 2.5–3 × 1.5 mm obovato-oblonga, extus et intus dense papillosa. Stamina isomorphica glabra; filamenta 2 mm longa; antherarum thecae 2–2.5 × 0.5 mm oblongae, poro ventraliter inclinato; connectivum nec prolongatum nec appendiculatum. Stylus 3.5–5 mm glaber; ovarium 5–6-loculare omnino inferum apice glabro.

Trees 4–9 m tall. Uppermost branchlets, vegetative buds, and inflorescences sparsely to moderately stellate-furfuraceous, the distal branchlet nodes bearing prominent interpetiolar lines or ridges. Leaves of a pair slightly unequal in size; petioles 0.8–2.1 cm long; blades membranaceous, 5–11.5 cm long and 2.5–4.1 cm wide, elliptic to elliptic-lanceolate, apex acuminate, base acute to obtuse, margin undulate-denticulate, 3(–5)-plinerved, the innermost pair of elevated primaries diverging from the median nerve in opposite or alternate fashion above the blade base, above glabrous at maturity, below essentially glabrous or sparingly and deciduously stellate-furfuraceous on the elevated primary nerves. Inflo-

rescence a terminal multiflowered panicle 5–10 cm long; bracts of the rachis nodes persistent, narrowly lance-triangular, 1–1.5 mm long, 0.25 mm wide at the base, sparingly stellulate-furfuraceous to glabrate; bracteoles sessile and persistent, subulate, 0.25–0.5 mm long, 0.25 mm wide, sparingly stellulate-furfuraceous, margin entire. Pedicels 0.5 mm long but lengthening to 1 mm in fruit, sparingly stellate. Hypanthia (at anthesis) campanulate, 2–2.5 mm long to the torus, sparingly and deciduously stellulate-furfuraceous to glabrous. Calyx tube ca. 0.5 mm long, truncate or obscurely undulate with 5 inconspicuous and early deciduous triangular calyx teeth ca. 0.25 mm long that barely project beyond calyx rim; torus glabrous adaxially. Petals 5, conspicuously papillose on both surfaces, white, obovate-oblong, rounded to irregularly undulate apically, 2.5–3 mm long, 1.5 mm wide distally. Stamens 10, isomorphic; filaments glabrous, complanate, 2 mm long; anthers 2–2.5 mm long, ca. 0.5 mm wide, erect to slightly incurved apically, yellow, linear-oblong, laterally compressed and deeply channeled ventrally between thecae, rounded at the apex with a ventrally inclined terminal pore; connective thickened dorsally but not prolonged or appendaged at the filament insertion. Ovary (at anthesis) completely inferior, 5–6-celled, globose to depressed-conic, the apex fluted and glabrous but becoming rounded in fruit. Style somewhat declinate and incurved distally, glabrous, 3.5–5 mm long; stigma punctiform to truncate. Berry globose, greenish-yellow when plump and fleshy, 4–5 mm long and 5–5.5 mm in diameter. Seeds irregularly pyramidal, 1.5 mm long, beige, smooth and vernicose with a rounded or bluntly angulate convex face.

PHENOLOGY.—Flowering and fruiting specimens have been collected from April through July and June through August, respectively.

DISTRIBUTION.—Rain forests of the municipalities of Catemaco and San Andrés Tuxtla in Veracruz, Mexico at 100–500 m.

ADDITIONAL SPECIMENS EXAMINED.—MEXICO, Veracruz: Municipio Catemaco, 6 km SW of Sontecomapan, 12 May 1972, *Beaman* 5953 (F, MEXU); Estación de Biología Tropical Los Tuxtlas, Cerro Vigía, 21 May 1981, *Gentry & Lott* 32208 (CAS, MEXU, MO, US); Municipio San Andrés Tuxtla, Laguna Escondida, 2 km NE of Estación de Biología Tropical Los Tuxtlas, 22 Jul. 1983, *Ibarra* 754 (CAS); Estación de Biología Tropical Los Tuxtlas, 95°04' and 95°09'W, 18°34' and 18°36'N, Lot 67, 24 Jun. 1984, *Ibarra & Cedillo* 1792 (CAS, TEX), Estación de Biología Tropical Los Tuxtlas, 95°04' and 95°09'W, 18°34' and 18°36'N, Lot 67, 21 Aug. 1984, *Ibarra*

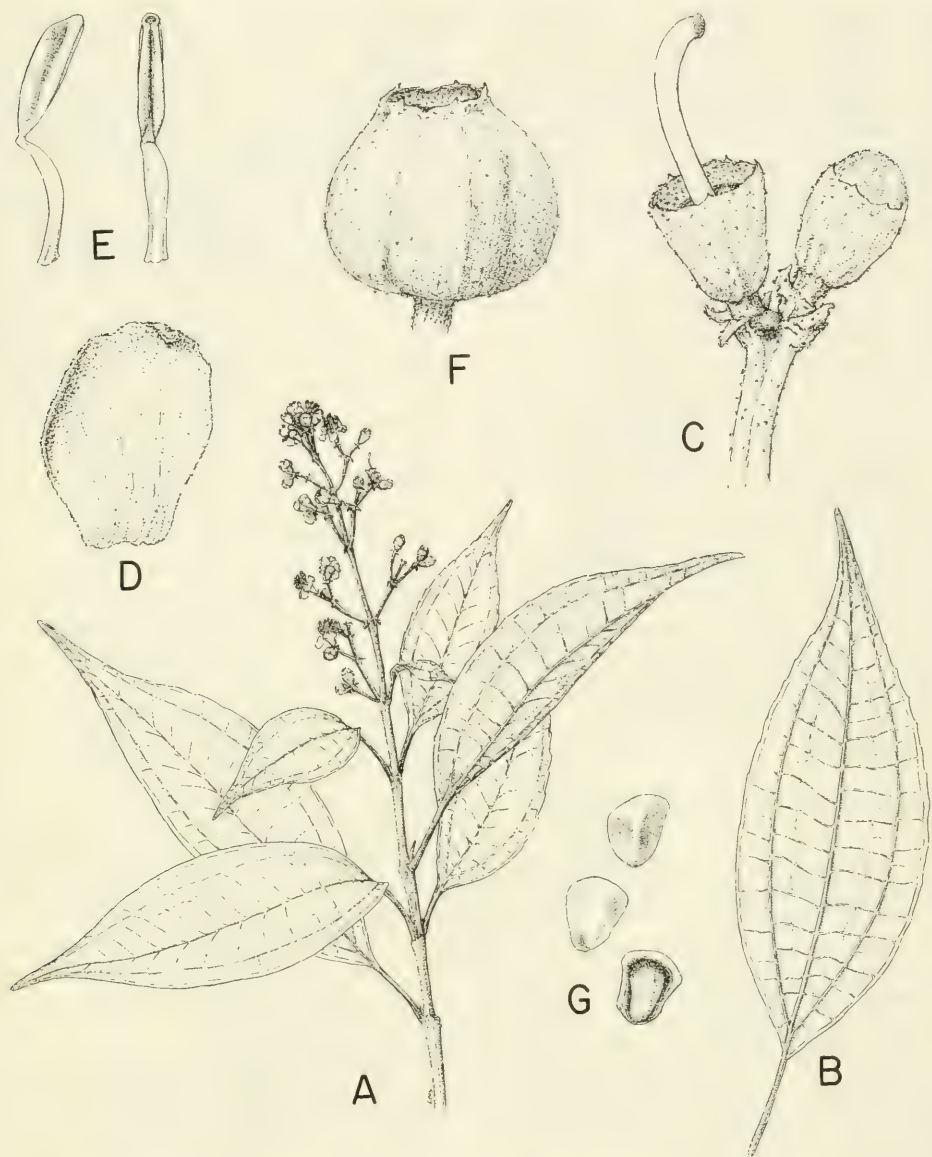


FIGURE 2. *Miconia ibarrae* Almeda. A, habit, $\times \frac{1}{2}$; B, representative leaf (lower surface), $\times \frac{1}{2}$; C, representative flower with petals and stamens removed (left) and floral bud (right), $\times$ ca. 7; D, petal (adaxial surface), $\times 9$; E, stamens, lateral view (left) and ventral view (right), $\times 8$; F, mature berry, $\times 6$; G, seeds, $\times$ ca. 6. (A–E from the holotype; F from *Ibarra* 754; G from *Ibarra* & *Sinica* 1931.)

& *Sinica* 1931 (CAS); Laguna Escondida, 2.5 km NE of Estación de Biología Tropical Los Tuxtlas, 95°04' and 95°09'W, 18°34' and 18°36'N, 23 Apr. 1985, *Ibarra et al.* 2407 (CAS).
This restricted species is defined by its sparse cover of white stellate-furfuraceous hairs on the lower leaf surfaces, prominent interpetiolar lines

or ridges on distal branchlets, undulate-denticulate leaves, truncate to obscurely undulate calyx, papillose petals, and irregularly pyramidate seeds that are smooth and vernicose on the rounded or bluntly angulate convex face. In leaf shape, calyx development, stamen morphology,

and petal details, *Miconia ibarrae* is most similar to *M. fulvostellata* L. O. Williams, a more widespread species that also occurs in the Los Tuxtlas region (Ibarra and Sinica 1987). In *M. fulvostellata*, the branchlets, petioles, lower leaf surfaces, inflorescences, and hypanthia (at anthesis) are densely covered with a ferrugineous stellate indument that conceals the surfaces of these structures. A superficial comparison of these two species may give the impression that *M. fulvostellata* is a densely pubescent extreme of *M. ibarrae*. However, *M. fulvostellata* also differs from the new species by a suite of other diagnostic characters: its style is straight, its stigma is capitate, and its pyramidal seeds have pusticulate angles on the convex face and a raphe on the concave side invested with a soft hyaline tissue that collapses irregularly when dry.

This species is named for Guillermo Ibarra M., coauthor of a useful checklist of the plants of the Tropical Biological Station at Los Tuxtlas, Veracruz. It was through his generosity that a fine set of flowering and fruiting material was made available for this study. In the published checklist, *M. ibarrae* is listed as *Miconia* sp. (Ibarra and Sinica 1987).

***Miconia iteophylla* Almeda, sp. nov.**

(Fig. 3)

TYPE.—PANAMÁ. Coclé: along Río San Juan below its junction with Río Tife, elev. 1,200 ft (366 m), 11 Jun. 1978, Hammel 3393 (holotype: CAS; isotype: MO).

Frutex 0.5–1.5 m. Ramuli primum obscure quadrangulati demum teretes sicut laminarum subtus venae primariae petioliculae modice granuloso-furfuraceae. Petioli 2–11 mm longi; lamina 4.5–9 × 0.6–1.7 cm anguste elliptica apice acuminata basi acuta vel acuminata, 3-plinervata, membranacea et integra. Panicula 2–7 cm longa multiflora; flores 5-meri, pedicellis (ad anthesim) 1–2 mm longis, bracteolis 0.5 × 0.25 mm persistentibus. Hypanthium (ad torum) 1–1.5 mm longum sparse caduceque granuloso-furfuraceum; calycis tubus 0.25 mm longus, lobis subtruncatus vel vix undulatus, dentibus exterioribus subulatis 0.25 mm eminentibus. Petala glabra 2–2.5 × 0.75 mm oblongo-elliptica apice rotundato. Stamina isomorphica glabra; filamenta 1–1.5 mm longa; antherarum thecae 1.25–1.5 × 0.25 mm angustae oblongae, poro paulo dorsaliter inclinato; connectivum nec prolongatum nec appendiculatum. Stylus 3.5 mm glaber; ovarium 5-loculare et $\frac{2}{3}$ inferum apicem versus sparse granuloso-puberulum.

Shrubs 0.5–1.5 m tall. Uppermost branchlets subquadrate to terete, moderately covered with a brown scurfy-pulverulent indument, the distal branchlet nodes bearing interpetiolar lines or ridges. Leaves of a pair somewhat unequal in

size; petioles 2–11 mm long; blades membranaceous, 4.5–9 cm long and 0.6–1.7 cm wide, narrowly elliptic, apex acuminate, base acute to acuminate, margin entire, 3-plinerved, the inner pair of elevated primaries diverging from the median nerve in opposite or subopposite fashion, the transverse secondaries prominulous and spaced 1–2(–3) mm apart at the widest portion of the blade, sparingly and deciduously scurfy-pulverulent above when young, deciduously scurfy-pulverulent on the elevated primaries and higher order venation below. Inflorescence a terminal multiflowered panicle 2–7 cm long typically branching 0.6–3 cm above the node initiating the inflorescence, the rachis beset with brown scurfy hairs; bracts of the rachis nodes sessile and persistent, 1.5–3.5 mm long, 0.25–0.5 mm wide, glabrous above, sparsely and deciduously scurfy-pulverulent below; bracteoles sessile and persistent, paired and fused laterally into a short nodal collar or elevated ridge, linear-oblong to narrowly and bluntly triangular, 0.5 mm long, ca. 0.25 mm wide, essentially glabrous. Pedicels 1–2 mm long, moderately to densely scurfy-pulverulent. Hypanthia (at anthesis) campanulate, 1–1.5 mm long to the torus, deciduously scurfy-pulverulent. Calyx tube 0.25 mm long, subtruncate, hyaline and entire, the lobes barely discernible as 5 depressed triangular undulations; exterior calyx teeth 5, subulate, 0.25 mm long, exceeding and obscuring the lobes, glabrous throughout; torus fimbriate-puberulent adaxially. Petals 5, glabrous, white, elliptic-oblong, rounded apically, 2–2.5 mm long, 0.75 mm wide. Stamens 10, isomorphic; filaments glabrous, complanate, 1–1.5 mm long; anthers 1.25–1.5 mm long, 0.25 mm wide, yellow, linear-oblong, truncate, rounded or emarginate at the apex with a somewhat dorsally inclined terminal pore; connective thickened dorsally but not prolonged or appendaged at the filament insertion. Ovary (at anthesis) $\frac{2}{3}$ inferior, 5-celled, globose, apex fluted and sparingly glandular puberulent but becoming rounded and glabrous in fruit. Style straight, glabrous, 3.5 mm long; stigma truncate to capitellate. Berry globose, red turning purple-black when mature, 2–4 mm long and 3–4 mm in diameter. Seeds irregularly angulate-pyramidal, 0.5 mm long, rusty brown, smooth, and vernicose with polished angles on the convex face.

PHENOLOGY.—Flowering specimens have been collected in June and July; fruiting collections

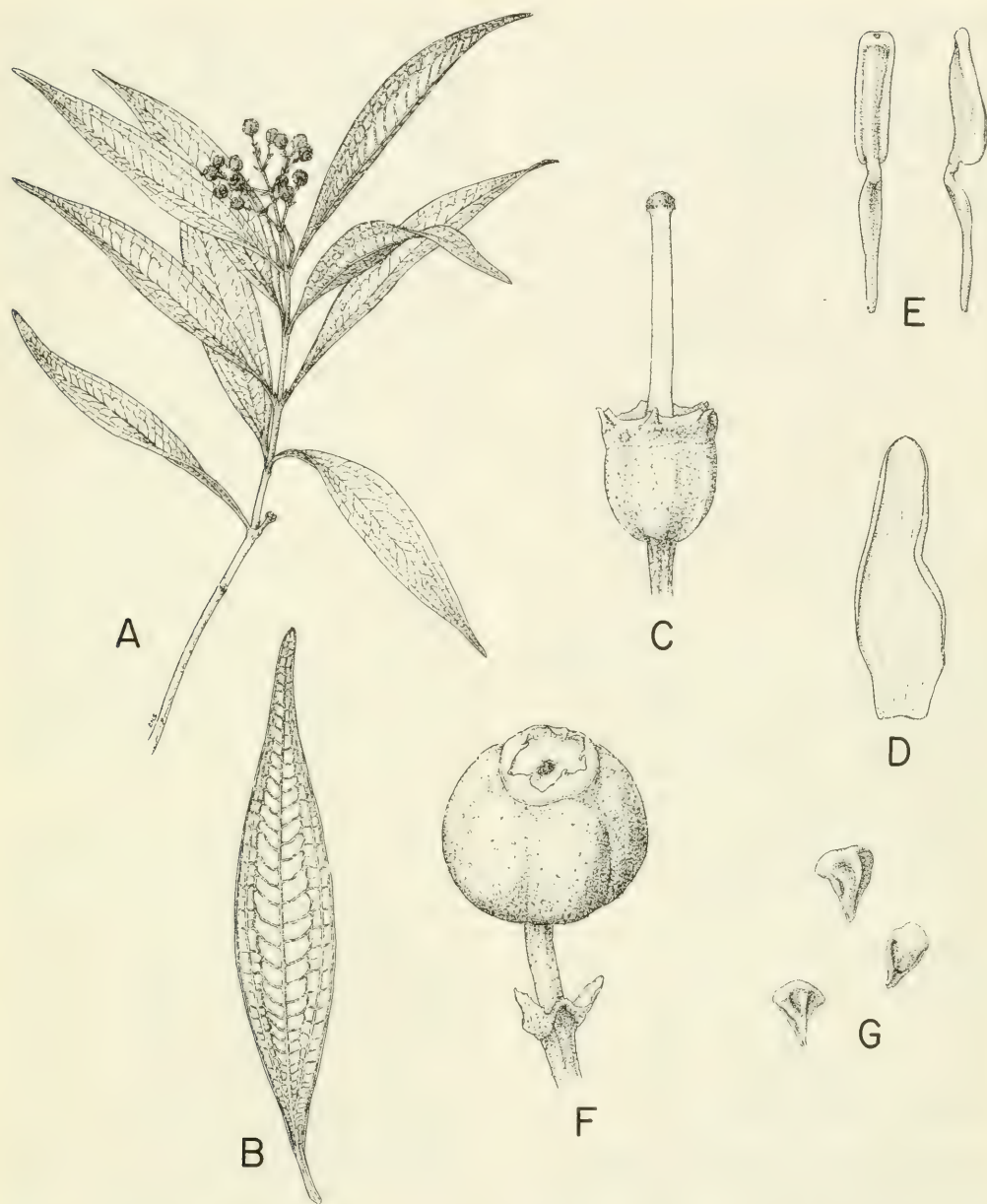


FIGURE 3. *Miconia iteophylla* Almeda. A, habit, $\times$ ca. 1; B, representative leaf (lower surface), $\times$ ca. 1; C, flower (at anthesis) with all petals and stamens removed, $\times$ 10; D, petal (adaxial surface), $\times$ 19; E, stamens, dorsal view (left) and lateral view (right), $\times$ ca. 14; F, mature berry, $\times$ ca. 7; G, seeds, $\times$ 20. (A–E from Hammel 3330; F from the holotype; G from Antonio 3669.)

have been made in February, June, and December.

DISTRIBUTION.—Rain forests on the Caribbean slope of Panamá in Bocas del Toro and Coclé provinces where it typically grows near moving water at 200–450 m.

ADDITIONAL SPECIMENS EXAMINED.—PANAMÁ. Bocas del Toro: upper Río San Pedro, 13 Jul. 1979, *Gordon 59Db* (MO). Coclé: trail from Caño Susio to Cerro Tife on the Atlantic slope, 3 Feb. 1980, *Antonio 3669* (CAS); Atlantic slope NW of El Copé, along Río San Juan near fork with Río Tife, 9 Jun. 1978, *Hammel 3330* (CAS); Caribbean side of divide at El Copé, 3 Feb. 1983, *Hamilton & Davidse 2628* (CAS); between

Caño Susio and waterfall at base of Cerro Tife, 13 Dec. 1980, Sytsma et al. 2541 (CAS).

Miconia iteophylla is distinguished by its brown scurfy-pulverulent indument, narrow elliptic leaves, linear-oblong petals, and pyramidate seeds with smooth polished angles on the convex face. It is related to a small group of species that includes *M. ligulata* and *M. peltata*, both of which are also treated herein. These three species share a scurfy-pulverulent indument, linear-oblong petals, a deciduously glandular puberulent ovary apex, and a torus that is puberulent adaxially. The brown scurfy indument is superficially similar in all of these taxa. In *M. iteophylla*, however, it consists of branlike scales unlike the pinoid hairs of *M. ligulata* and *M. peltata*. The seeds of *M. iteophylla* and *M. peltata* are identical in shape and sculptural details which suggests that these two species may be more closely related to one another than either is to *M. ligulata*. In general aspect *M. iteophylla* resembles *M. ligulata*, which is readily differentiated by its larger (12–28 × 4–10 cm) 5-plinerved leaf blades that are decurrent on the petiole, and pyramidate seeds with verruculose angles on the convex face.

The epithet for this species is derived from the Greek words *itea*, willow, and *phyllon*, leaf, in reference to the narrow willowlike leaf blades. This species is referred to locally as “ugua” (fide Gordon 59Db, MO) by the Guaymí, the largest Indian group in Panamá (Gordon 1982).

Miconia ligulata Almeda, nom. nov.

Leandra consimilis Gleason, Ann. Missouri Bot. Gard. 45:268. 1958.

TYPE.—PANAMÁ. Las Minas, Allen 2702 (holotype: NY). Non *Miconia consimilis* Pilger, Verh. Bot. Ver. Brand. 47:170. 1905. This latter entity is a taxonomic synonym of *Graffenrieda gracilis* (Triana) L. O. Williams (Williams 1963; Wurdack 1970).

In the protologue, Gleason described the petals of this species as oblong-lanceolate. This is understandable in view of the fact that the distal petal margins tend to become involute and superficially appear acute when pressed and dried. Traditionally berry-fruited species in the *Miconieae* with terminal inflorescences and acute petals have been placed in *Leandra*. The petals of *Leandra consimilis* are actually linear-oblong and rounded to obtuse apically like several described species in *Miconia*. To rectify its taxonomic placement, *Leandra consimilis* is here trans-

ferred to *Miconia*. This requires the adoption of a new name because the epithet *consimilis* is already pre-empted in *Miconia*. When Gleason described this species it was known from only the Panamánian holotype. Wurdack (1978) reported it from Costa Rica south to Venezuela and I have recently recorded that its range extends northward to Nicaragua (Almeda, in press). An expanded description is provided here to reflect the range of variation exhibited by the species throughout its known range.

Shrubs or small trees (1.5–)4–9 m tall. Uppermost branches rounded-quadrate to quadrisulcate, the young branchlets, petioles, primary leaf veins below, and inflorescences moderately to densely covered with a brown scurfy indument of pinoid hairs. Leaves of a pair equal to somewhat unequal in size; petioles 0.7–2.5 cm long; blades membranaceous, 12–28 cm long and 4–10 cm wide, elliptic, apex attenuate to long-acuminate, base gradually tapering and decurrent on the petiole, margin entire to undulate, 5-plinerved, the innermost pair of elevated primaries diverging from the median nerve in opposite or alternate fashion, the transverse secondaries prominulous and spaced 3–7 mm apart at the widest portion of the blade, sparsely scurfy-pulverulent to glabrate above, moderately and deciduously scurfy-pulverulent on the secondary and higher order veins below. Inflorescence a terminal multiflowered panicle 4–11.5 cm long typically branching (0.5–)1.5–3.5 cm above the node initiating the inflorescence; bracts of the rachis nodes persistent, 1–5 mm long, 0.25–1 mm wide, glabrous above, moderately covered with scurfy-pulverulent or short-stalked pinoid hairs below; bracteoles sessile and persistent, paired and fused laterally to form a nodal ridge or shallow collar, narrowly triangular, 0.5 mm long, 0.25–0.5 mm wide, glabrous above and sparingly scurfy-pulverulent to glabrate below. Pedicels 0.5–1 mm long with an indument like that of the bracteoles. Hypanthia (at anthesis) campanulate, 1–1.5 mm long to the torus, deciduously scurfy-pulverulent to stellulate-furfuraceous. Calyx tube 0.25 mm long, subtruncate, hyaline, and entire or undulate with 5 rounded-triangular lobes 0.25 mm long; exterior calyx teeth 5, subulate, 0.25 mm long, equaling or exceeding and obscuring the lobes, glabrous throughout; torus sparsely fimbriate-puberulent or glandular puberulent adaxially. Petals 5, glabrous, white,

linear-oblong, obtuse to rounded apically, 2–3.5 mm long, 0.75–1 mm wide. Stamens 10, isomorphic; filaments glabrous, complanate, 1 mm long; anthers 0.75–1.25 mm long, 0.25 mm wide, yellow, linear-oblong, truncate to slightly emarginate at the apex with a somewhat dorsally inclined terminal pore; connective thickened dorsally but not prolonged or appendaged at the filament insertion. Ovary (at anthesis) $\frac{3}{4}$ to $\frac{5}{8}$ inferior, 5-celled, globose, apex lobed or fluted and sparsely glandular puberulent but becoming rounded and glabrous in fruit. Style straight, glabrous, 3–4 mm long; stigma truncate but not conspicuously dilated. Berry globose, pink but turning blue-purple when mature, 2–4 mm long and 3–4 mm in diameter. Seeds angular-pyramidal, ca. 0.5 mm long, brown, smooth with verruculose angles on the convex face.

PHENOLOGY.—Flowering sporadically from January through October; fruiting specimens have been collected from August through January.

DISTRIBUTION.—Widespread in wet evergreen forests on the Caribbean slope of Central America from eastern Nicaragua (Zelaya) south and east through Costa Rica and Panamá to north-western Venezuela (Zulia) from sea level to 1,100 m.

REPRESENTATIVE SPECIMENS EXAMINED.—NICARAGUA. Zelaya: SW flank of Cerro Hormiguero, 18 Apr. 1979, *Grijalva 440* (CAS). COSTA RICA. Alajuela: between San Lorenzo and Los Angeles de San Ramon, above Río San Lorenzo, 10°14'N, 84°32'W, 20 Sep. 1978, *Burger & Antonio 11176* (CAS). Heredia: road between Puerto Viejo and La Virgen, near Chilamate, 30 May 1982, *Hammel 12670* (CAS); Finca La Selva, the OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, 1 Aug. 1980, *Hammel 9403* (CAS). Limón: 2 airline km SSE of Islas Buena Vista in the Río Colorado, 83°40'W, 10°40'N, 13–14 Sep. 1986, *Davidse & Herrera 31064* (CAS); Hacienda Tapezco-Hda. La Suerte, 29 air km W of Tortuguero, 10°30'N, 83°47'W, 22 Aug. 1979, *Davidson & Donahue 8665* (CAS); Cerro Coronel, E of Río Zapote, along and above new road within 1 km of Río Colorado, 10°40'N, 83°40'W, 13–14 Sep. 1986, *Stevens & Montiel 24356* (CAS). PANAMÁ. Coclé: La Mesa above El Valle de Anton, N of Cerro Gaital, 8°37'N, 80°06'W, 26 Jul. 1984, *de Nevers et al. 3524* (CAS); foothills and summit of Cerro Caracoral, near La Mesa and N of El Valle de Anton, 10 Sep. 1981, *Knapp 1092* (CAS); Atlantic slope of the Continental Divide near sawmill above El Copé, 8°40'N, 80°36'W, 13 Feb 1982, *Knapp & Dresler 3506* (CAS); Río Guanche, 9°30'N, 79°39'W, 15 Oct. 1980, *Sytma 1666* (CAS). Comarca de San Blas: El Llano-Cartí Road, Continental Divide, 9°19'N, 78°55'W, 25 Aug. 1984, *de Nevers 3760* (CAS). Darién: Cerro Pirre valley between Pirre and next most southerly peak, 10–20 Jul. 1977, *Folsom 4429* (CAS). Panamá: top of Cerro Campana, 8 Sep. 1982, *D'Arcy 15092* (CAS); Pipeline road, N of Gamboa, 9°10'N, 79°45'W,

4 Aug. 1984, *de Nevers & Hews 3635* (CAS). VENEZUELA. Zulia: Caño Helena, Sierra Perijá, *Delascio & Benkowski 3197* (US.)

Miconia ligulata belongs to the group of three species discussed above under *M. iteophylla*. Among its close allies it is unique in having wide leaf blades (4–10 cm) that are gradually tapered at the base and decurrent on the petiole. The verruculose angles on the convex seed face constitute another distinctive but less conspicuous feature of *M. ligulata*. The new name for this species is derived from *ligula*, Latin for little tongue or strap, in reference to the elongate strap-like petals.

Miconia peltata Almeda, sp. nov.

(Fig. 4)

TYPE.—PANAMÁ. Panamá: near Cerro Jefe, along road towards Alto Pacora, forested slopes ca. 850 m, ca. 9°15'N, 79°30'W, 27 Dec. 1985, *McPherson 7882* (holotype: CAS; isotype: MO).

Frutex vel arbor parva 3–6 m. Ramuli primum paulo compressi demum teretes sicut petioli foliorum subtus venae primariae inflorescentiaque pilis pinoideis ca. 0.25 mm longis plus minusve caducis dense induti. Petioli 1.3–5 cm longi; lamina peltata 6.7–14.5 × 3.3–8.3 cm ovata vel elliptico-ovata apice acuminata basi rotundata vel subcordata, 5–7-nervata, subcoriacea et undulato-denticulata vel subintegra. Inflorescentia 3–4 cm longa multiflora, ramis oppositis divaricatis; flores 5-meri, pedicellis (ad anthesim) 1 mm longum, pilis plerumque breviuscule stipitato-stellatis vel stellulato-pinoideis praeditum. Calycis tubus 0.25 mm longus, lobis ca. 0.25 mm altis late triangularibus, dentibus exterioribus triangularibus 0.25 mm eminentibus. Petala glabra 2.5 × 0.5 mm oblonga-elliptica apice rotundato vel rotundato-obtusio. Stamina isomorphica glabra; filamenta 1 mm longa; antherarum thecae 0.75–1 × 0.25 mm anguste oblongae, poro paulo dorsaliter inclinato; connectivum nec prolongatum nec appendiculatum. Stylus 1.5 mm glaber; ovarium 5-loculare et $\frac{2}{3}$ inferum apice sparsiuscule glanduloso-puberulo.

Shrubs or small trees 3–6 m tall. Uppermost branchlets compressed and two-sided but becoming rounded with age. Distal branchlets, petioles, primary leaf veins below, and inflorescences densely and somewhat deciduously covered with a rusty brown indument of pinoid hairs. Leaves of a pair somewhat unequal in size, peltate with the petiole attached 5–8 mm from the basal edge, petioles 1.3–5 cm long; blades subcoriaceous, 6.7–14.5 cm long and 3.3–8.3 cm wide, ovate to elliptic-ovate, apex acuminate, base broadly rounded to subcordate, margin inconspicuously undulate-denticulate to subentire, 5–7-nerved abaxially, the transverse secondaries prominent and 2–3 mm apart at the widest

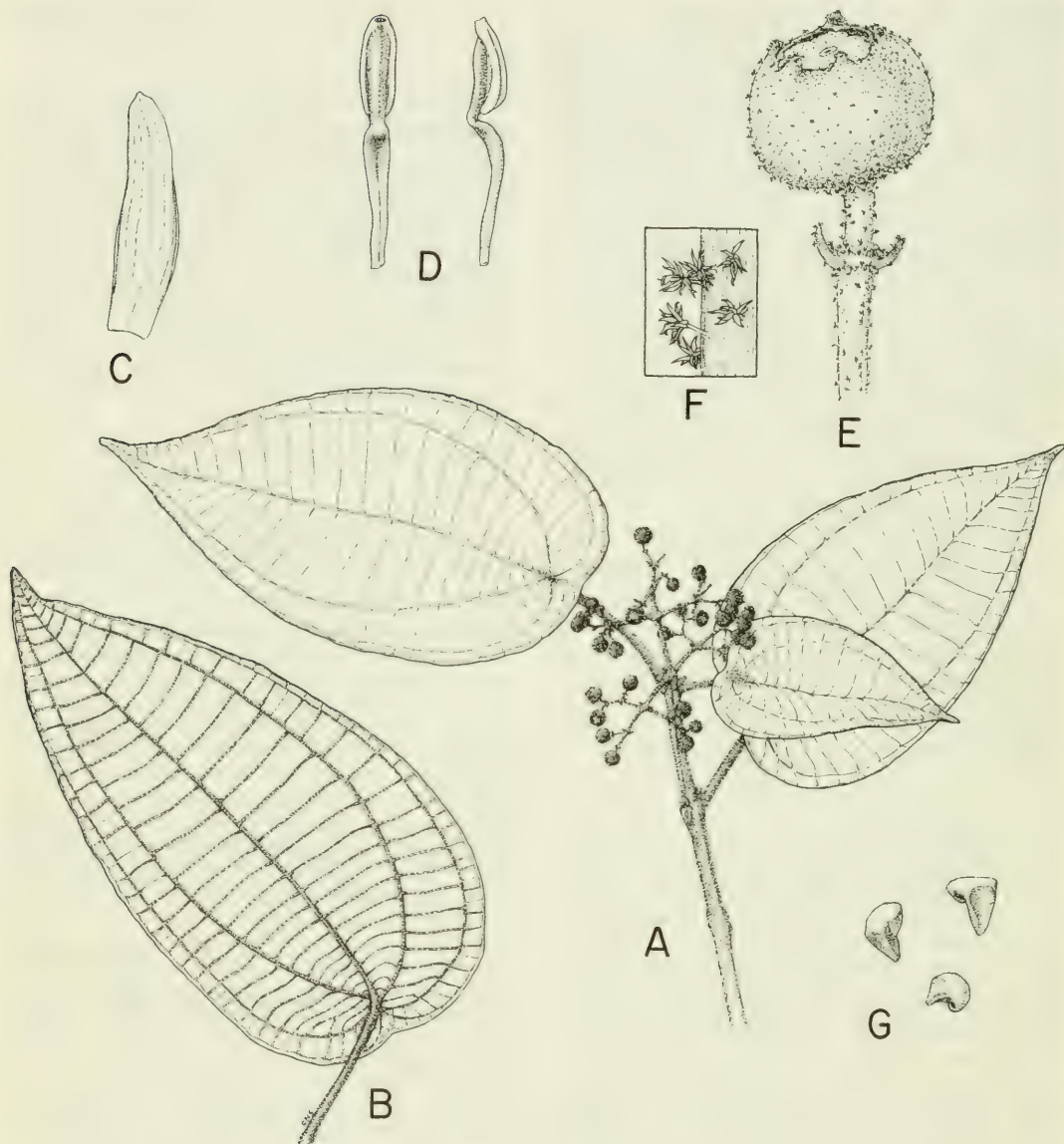


FIGURE 4. *Miconia peltata* Almeda. A, habit, $\times$ ca. $\frac{2}{3}$; B, representative leaf (lower surface), $\times$ ca. $\frac{2}{3}$; C, petal (adaxial surface), $\times$ 12; D, stamens, dorsal view (left) and lateral view (right), $\times$ ca. 17; E, mature berry and bracteoles, $\times$ 6; F, enlargement of pinoid hairs on fruiting pedicel, $\times$ ca. 60; G, seeds, $\times$ 16. (A, B, E, F from Tyson 3440; C, D, G from the holotype.)

portion of the blade, glabrous above, the secondaries and higher order veins below sparingly beset with spreading pinoid hairs and an inconspicuous appressed glandular puberulence. Inflorescence a multiflowered paniculiform dichasium 3–4 cm long divaricately branched from the base; bracts of the rachis nodes sessile and

persistent, 1.5–4 mm long, 0.5 mm wide, sparsely beset with pinoid hairs; bracteoles sessile and persistent, subulate, 0.25–0.5 mm long, mostly less than 0.25 mm wide, essentially glabrous throughout. Pedicels 1 mm long. Hypanthia (at anthesis) campanulate to subglobose, 1.5 mm long to the torus, moderately to sparsely covered

TABLE 1. Comparison of chromosome numbers, pollen size, and ecogeographic ranges in *Pilocosta*.

	Haploid number	Pollen diameter	Ecogeographic range
<i>P. campanensis</i>	n = 11	16.5–18.8 μm	Central Panamá at 300–1,000 m
<i>P. erythrophylla</i>	n = 7, 14	14.1–16.5 μm	Central Costa Rica at 1,480–2,000 m
<i>P. nana</i>	n = 33	25.5–30.6 μm	Costa Rica through central Panamá to Colombia (Magdalena) and Ecuador (Pichincha) at 450–1,800 m
<i>P. oerstedii</i>	n = 18	17.6–21.2 μm	Central Costa Rica to western Panamá at 900–2,000 m

with stipitate-stellate or short pinoid hairs. Calyx tube 0.25 mm long, subtruncate, hyaline and entire, with 5 triangular lobes ca. 0.25 mm long; exterior calyx teeth 5, bluntly triangular, 0.25 mm long, glabrous throughout; torus inconspicuously fimbriate puberulent adaxially. Petals 5, glabrous, reddish-pink, oblong-elliptic, rounded to obtuse apically, 2.5 mm long, 0.5 mm wide. Stamens 10, isomorphic; filaments glabrous, complanate, 1 mm long; anthers 0.75–1 mm long, 0.25 mm wide, pale yellow, oblong, rounded to subtruncate at the apex with a somewhat dorsally inclined terminal pore; connective thickened dorsally but not prolonged or appendaged at the filament insertion. Ovary (at anthesis) $\frac{2}{3}$ inferior, 5-celled, globose, apex fluted and sparingly glandular puberulent but rounded and glabrous in fruit. Style straight, glabrous, 1.5 mm long; stigma truncate. Berry globose, purple when mature, 2–2.5 mm long and 3–4 mm in diameter. Seeds irregularly angulate-pyramidal, 0.5 mm long, brown, smooth with polished angles on the convex face.

PHENOLOGY.—Flowering and fruiting specimens have been collected in October, December, and February.

DISTRIBUTION.—Endemic to Cerro Jefe in central Panamá at 850–1,000 m.

ADDITIONAL SPECIMENS EXAMINED.—PANAMÁ. Panamá: Cerro Jefe, 7 Oct. 1986, *Aranda & Valdespino 185* (CAS, MO, PMA); E slope of Cerro Jefe, 8 Feb. 1966, *Tyson 3440* (MO—2 sheets).

Miconia peltata also belongs to the group of three species discussed above under *M. iteophylla*. Because of its ovate to elliptic-ovate peltate leaves it is recognizable even in sterile condition. In addition to its unusual leaves, *M. peltata* differs from closely allied species in having reddish-pink petals and an inflorescence that is divaricately branched from the base. The epithet *peltata* is derived from the Greek word, *pelte*,

small shield. This refers to the attachment of the petioles to the lower foliar surface away from the margin of the blade.

***Pilocosta campanensis* (Almeda & Whiffin) Almeda, stat. nov.**

Pilocosta oerstedii (Triana) Almeda & Whiffin subsp. *campanensis* Almeda & Whiffin, Syst. Bot. 5(3):306. 1980 [1981].

TYPE.—PANAMÁ. Panamá: Cerro Campana, 10 Dec. 1967, *Lewis et al. 3069* (holotype: MO!; isotypes: COL, DUKE!, FI, K!, NY!, UC!).

When Trevor Whiffin and I described this as a subspecies of *Pilocosta oerstedii* we based our decision on similarities in habit and androecial details (Almeda and Whiffin 1981). We also entertained the possibility of describing it as a subspecies of *P. nana* because of similarities in the kind and distribution of hypanthial pubescence. At the time it was the only taxon in the genus for which we had no chromosome information. Based on information then available we recognized two subspecies under *P. oerstedii* because of their non-overlapping geographic distribution and elevational displacement. A recent study of chromosome numbers in neotropical Melastomataceae (Almeda and Chuang, in prep.) reveals that this taxon has a haploid number of $n = 11$ (count based on field collected buds of *Almeda et al. 5880*, CAS). Based on morphological, cytological, and ecogeographic data, it is clear that *Pilocosta oerstedii* subsp. *campanensis* has all the attributes that characterize species in this genus (Table 1). I therefore elevate it to species status. An alternative disposition would be to make it a subspecies of *P. nana*. This, however, would make no sense in view of their pronounced morphological and cytological differences and the fact that I have found individuals of these two taxa growing next to one another near La Mesa in Coclé Province, Panamá.

A chromosome number of $n = 11$ in *P. campanensis* reconfirms our previous assertion regarding the complex cytological evolution within this small natural genus. It also sheds new light on the relationship of *P. nana* and provides some clues on the evolutionary polarity of character states judged to be of taxonomic value in *Pilocosta*. With $n = 33$, *P. nana* appears to be a hexaploid derivative of *P. campanensis*. The polyploid gain in *P. nana* has evidently been accompanied by the derivation of an herbaceous habit and subisomorphic androecium from the woody habit and dimorphic androecium of *P. campanensis*.

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REVIEW OF THE EELPOUT GENUS
PACHYCARA ZUGMAYER, 1911 (TELEOSTEI: ZOARCIDAE),
WITH DESCRIPTIONS OF SIX NEW SPECIES

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ABSTRACT: The eelpout genus *Pachycara* Zugmayer, 1911 is revised to include 12 species, 6 of which are reported here as new: *P. shcherbachevi* from the Indian Ocean; *P. sulakai* and *P. crossacanthum* from the Atlantic; and *P. mesoporum*, *P. pammelae*, and *P. rimae* from the Pacific. *Pachycara* is a primitive lycodine eelpout genus characterized by its large body size, small head pores, lack of mental crests, and low parasphenoid wing. It is most closely related to *Lycodes* Reinhardt, 1832, and *Thermarces* Rosenblatt and Cohen, 1986. The species of *Pachycara* are characterized by their lateral line patterns, variably present or absent pelvic fins, counts of the axial skeleton, gill raker morphology, head pore patterns, and branchiostegal ray number. The genus is distributed in the eastern Pacific, Antarctic, Atlantic and Indian oceans from the upper continental slope to the abyss (200-4,780 m).

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INTRODUCTION

The eelpout genus *Pachycara* was erected by Zugmayer (1911a, b) for a species known from a single specimen taken in the abyssal North Atlantic. Anderson (1988a) considered the Antarctic genus *Austrolycichthys* Regan, 1913 a junior synonym of *Pachycara*, broadening the diagnosis chiefly by rejecting the presence or absence of pelvic fins as a generic character in eelpouts (see also Anderson 1988b). Anderson and Peden (1988) reported the genus from the North Pacific for the first time, further broadening its limits, and described two new species. They cited my unpublished dissertation (Anderson 1984) as a source of information on the genus. This paper is an update of that study, revised to include 12 species, six of which are new.

Considerable taxonomic confusion exists in the literature on eelpouts, especially for the rare deep-sea species. As was found earlier (Anderson 1982a), comparison of recently collected specimens of *Pachycara* with older, published material was difficult because of a lack of, or poor state of, types and the use of non-diagnostic characters by previous authors. As a contribution to the clarification of the systematics of *Pachycara*, I provide descriptions and/or diagnoses for all species, list synonymies, provide a key, distributional maps and illustrations to facilitate identification, and compare *Pachycara* to its putative sister genera.

Prior to the postwar rejuvenation of deep-sea exploration, specimens here referred to *Pachycara* were few in collections, and, in fact, consisted only of the types of *P. bulbiceps* (Garman,

1899) (= *P. obesa* Zugmayer, 1911), *P. suspectum* (Garman, 1899), *P. crassiceps* (Roule, 1916), and about 60 specimens of *P. brachycephalum* (Pappenheim, 1912). The more important recent collections of deep-sea fishes that resulted in the capture of *Pachycara* specimens are briefly discussed below.

Specimens from the Pacific Ocean were first taken during the round-the-world expedition of the Danish ship GALATHEA which collected the rare *P. suspectum* in the Gulf of Panama in 1952. This expedition had in the previous year collected the holotype of *P. shcherbachevi* in the Bay of Bengal. The bulk of the North Pacific species were taken by free vehicle set line traps by personnel of the Scripps Institution of Oceanography off Mexico and southern California, by bottom trawls operated from ships of Oregon State University, and by Canadian experimental sablefish (*Anoplopoma fimbria*) traps off the Queen Charlotte Islands (summarized in Anderson and Peden 1988). Specimens from the southeastern Pacific have come from operations of DSV ALVIN in the Galapagos Rift Zone (Cohen and Haedrich 1983), Chilean fisheries reconnaissance, supplied to the author by Ismael Kong, University of Antofagasta, and deep-sea bottom trawls by the ship ANTON BRUUN during the National Science Foundation's Southeastern Pacific Biological Oceanographic Program (SEBPBP). Explorations in the Atlantic Ocean began with the capture of the type species, *P. obesa* (= *P. bulbiceps*) by the expeditions of Prince Albert I of Monaco in the Bay of Biscay (Zugmayer 1911a, b). Subsequently, other eastern Atlantic material has come from expeditions of the Institute of Oceanographic Sciences, U.K. (Merrett and Marshall 1981), the BENGUELA VII expedition of the Instituto de Investigaciones Pesqueras de Barcelona (now Instituto de Ciencias del Mar), fish trapping cruises of the Office de la Recherche Scientifique et Technique Outre-Mer, Dakar, Senegal, exploratory fisheries cruises of the USSR (Golovan' 1978), and similar cruises by the South African ship AFRICANA around the Cape of Good Hope. Specimens of *Pachycara* from the northwestern Atlantic are relatively few and were taken by bottom trawls in the Middle Atlantic Bight (Musick 1979; Haedrich et al. 1980), the Caribbean Sea (Anderson et al. 1986), by bottom traps around Puerto Rico, supplied to the author by Dannie A. Hensley,

University of Puerto Rico, and from operations of DSV ALVIN in the Gulf of Mexico (Paull et al. 1984).

METHODS AND MATERIALS

Measurements were made with dial calipers or ocular micrometer to the nearest 0.1 mm. Osteological observations were made on cleared and stained specimens (Dingerkus and Uhler 1977) and drawings made with the aid of a camera lucida. Definitions of characters and measurements follow those of Anderson (1982a, 1984). Institutional abbreviations are as listed in Leviton et al. (1985), or as emended by Leviton and Gibbs (1988).

This review is based on 249 specimens, 76–597 mm standard length (SL), housed in 21 museum collections in 12 countries (listed by abbreviation in each account; measurements of specimens in SL). All type specimens were examined except the holotype of *Lycenchelys crassiceps* Roule, 1916, thought to be lost. A lectotype of *Lycodes brachycephalus* Pappenheim, 1912, is selected. Full accounts and illustrations are provided for all species except those recently reviewed (*P. brachycephalum* [see Anderson 1988a], *P. bulbiceps*, *P. gymninium*, *P. lepinium*, and *P. suspectum* [see Anderson and Peden 1988]), but expanded diagnoses for these species are provided which include other, important characters, for ease of reference under one cover. The osteological section of the description of the genus is intentionally brief, and the reader should consult Anderson (1982a) for a more thorough account of a generalized zoarcid (which includes *Pachycara*).

Species accounts are presented alphabetically by ocean basin in the following order: Atlantic, Indian, Pacific, and Antarctic.

Abbreviations for bone names used in the text figures are as follows:

act—actinosts
ang—anguloarticular
boc—basioccipital
br r—branchiostegal ray
cerhy—ceratohyal
cl—cleithrum
cor—coracoid
den—dentary
ect—ectopterygoid
epihy—epihyal

epo—epioccipital (epiotic)
 exo—exoccipital
 fr—frontal
 hyom—hyomandibula
 hyphy—hypophyals
 inop—interopercle
 inthy—interhyal
 lat eth—lateral ethmoid
 mes—mesethmoid
 met—metapterygoid
 op—opercle
 pal—palatine
 par—parietal
 pas—parasphenoid
 pcl—postcleithrum
 pel—pelvic (basipterygium)
 pmx—premaxilla
 pop—preopercle
 ptem—posttemporal
 pto—pterosphenoid
 pts—pterosphenoid
 quad—quadrate
 scap—scapula
 sop—subopercle
 sph—sphenotic
 supcl—supracleithrum
 urhy—urohyal

Pachycara Zugmayer, 1911

Pachycara Zugmayer, 1911a:12 (original description; expanded in Zugmayer, 1911b:134–136, pl. VI, fig. 6. Type species: *Pachycara obesa* Zugmayer, 1911 (= *Maynea bulbiceps* Garman, 1899), by monotypy.
Austrolycichthys Regan, 1913:244–245, fig. 2 (type species: *Lycodes brachycephalus* Pappenheim, 1912, by subsequent designation of Jordan, 1920:550).
Pachycarichthys Whitley, 1931:334 (improper emendation).
Pachychara (lapsus calami). Fowler, 1936:1056, fig. 437; Andriashev, 1986:170, text fig.

DIAGNOSIS.—Body robust, tail short; skin firm; mental crests (cartilaginous ridges on dentary) absent; parasphenoid wing not extending above mid-height of trigeminofacialis foramen; palatopterygoid (palatal) arch well developed, with ectopterygoid and mesopterygoid broadly articulating with quadrate; cephalic lateralis pores few, small, rounded; precaudal vertebrae 21–32; suborbital bones 6–8; pelvic fins present or absent, their presence individually variable in two species; scales, body lateral line, vomerine and palatine teeth, pseudobranch (except in one species), and pyloric caeca present.

DESCRIPTION.—Head large, ovoid, snout generally bluntly rounded, never dorsoventrally depressed in adults; young juveniles with somewhat depressed heads, but snout not as long and tapering as lycenchelyine (Anderson 1984) genera. Largest males with wider head than in females owing to greater development of adductor mandibulae (in those species with sample size large enough to test statistically). Body elongate, robust, subcircular in cross-section, its greatest depth midway between pectoral base and anus; body height at anal fin origin 7.7–16.9% SL in specimens over 160 mm SL. Tail high, increasingly laterally compressed posteriad. Skin firm, not gelatinous, covering all fins. Scales minute, cycloid, imbedded, covering body usually including abdomen (except in smallest specimens and *P. rimae*), bases of vertical fins, pectoral base and pectoral axil. Complete mediolateral and ventral (Andriashev 1954, fig. 142) lateral line(s) developed as single row of superficial neuromasts (“free lateralis organs”; Springer and Freihof 1976), their origins variable and usually species specific. Eye large and ovoid in young, often relatively small and rounded in adults, often entering dorsal profile of head. Nostril single, tubular, at snout tip, nasal tube not reaching upper lip except in some young. Pectoral fin large, of 14–19 rays, middle rays longest in large specimens, lowermost rays thickened, slightly exserted at tips. Pectoral base low on body, its origin just below midline, insertion on abdomen. Gill slit extending ventrally to lower margin of pectoral base or below. Ovary single. Pseudobranch filaments 2–7 (absent in *P. rimae*). Two nublke pyloric caeca, usually better defined in young. Stomach and intestines pale. Peritoneum black. Reproductive mode unknown, probably oviparous.

Mouth terminal or subterminal, lips fleshy but not thickened. Upper lip free across snout, lower lip adnate at dentary symphysis. Oral valve (palatal membrane) moderately developed, usually reaching anterior margin of vomer, but often constricted at sides except in very small specimens.

Cephalic lateralis pores small, rounded, relatively few. Six (usually; eight in *P. crassiceps*) suborbital bones from which arise 5–7 pores. One to four postorbital pores present, their number, like those of suborbitals, individually variable within a species. Two nasal (anterior supraor-

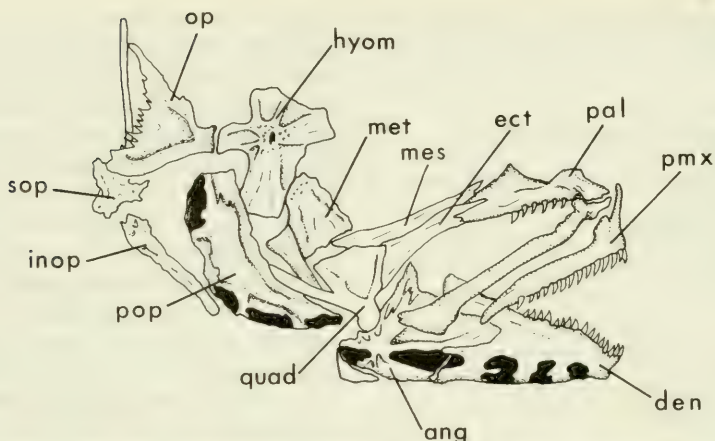


FIGURE 1. Jaws, suspensorium, and opercular bones of *Pachycara bulbiceps*, BMNH 1981.6.16:15, 332 mm SL; right lateral view.

bital) pores present at snout tip arising from foramina in anterior and posterior ends of nasal bone. Interorbital pore(s) absent. Occipital pores absent except in *P. mesoporum* and in two of six specimens of *P. crossacanthum*. Preopercular and mandibular canals joined; preoperculomandibular pores and bone foramina system in plesiomorphic state for family (and no variation noted), with four pores emanating from dentary, one from anguloarticular, and three from preopercle (Fig. 1). Head speckled with small, white superficial neuromasts, particularly on nape and cheeks; no pattern to these discernible.

Neurocranium well ossified, somewhat box-like (Fig. 2). Lateral ethmoid broad, not strongly decurved, but deeply sculptured at surface for attachment of palatine ligaments. Anterior, cup-shaped section of mesethmoid broad, deep. Parasphenoid wing low, not reaching mid-height of trigeminofacialis foramen, broadly articulating with frontal and pterosphenoid. Pterosphenoid almost completely forming anterior border of trigeminofacialis foramen. Frontals unfused, with deep, open channel anteriorly passing supraorbital lateralis canal. Sphenotic and parietal separated by frontal and pterotic. Lateral protuberance for attachment of levator arcus palatini muscle a weak ridge. Parietals separated from midline by supraoccipital, with no channel through posterior margin bracing supratemporal commissure (which is incomplete or absent in all but two species). Supraoccipital large, anterior ramus extending well under frontals, mesial crest low; supraoccipital narrowly contacting exoccip-

ital posteriorly. Prootic and sphenotic articulating dorsally forming hyomandibular condyle. Hyomandibular foramen well separated from condyle (Fig. 2A). Prootic also articulating dor-

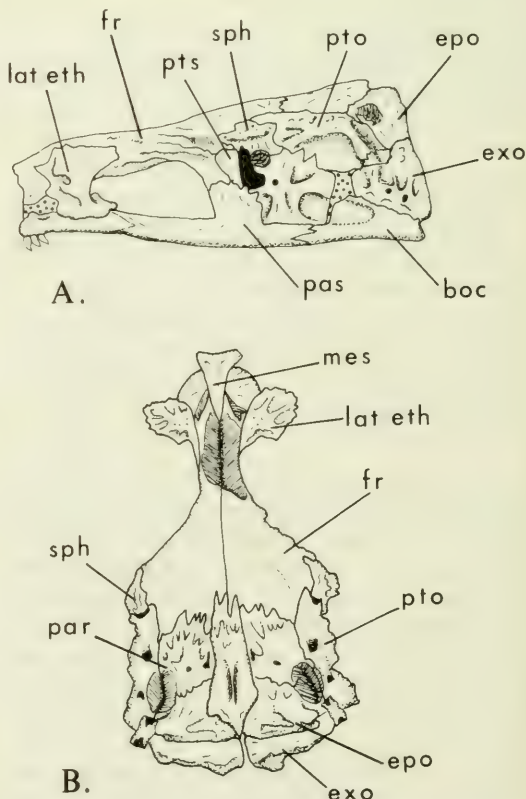


FIGURE 2. Neurocranium of *Pachycara gymminium*, BCPM 980-100, 281 mm SL; (A) left lateral view; (B) dorsal view.

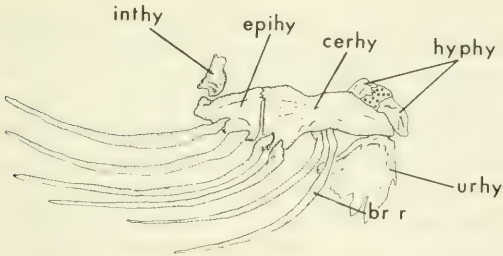


FIGURE 3. Right hyoid bar of *Pachycara gymninium*, BCPM 980-100, 281 mm SL; lateral view.

sally with pterotic and intercalar, which form a ridge extending onto exoccipital. Single pair of small, barrel-like lateral extrascapulars present. Foramina passing ninth (glossopharyngeal) and tenth (vagus) cranial nerves located on low, lateral ridge well away from margins of exoccipital.

Teeth present on jaws (absent on maxilla), vomer, palatine and pharyngeal bones. Palatopterygoid (palatal) arch well developed, ectopterygoid and mesopterygoid broadly overlapping anterior and dorsal margins of quadrate (Fig. 1). Hyomandibular posterior ramus not elongated. Opercle (posteriorly) and subopercle poorly ossified. Metapterygoid relatively large and thick.

Most or all of ceratohyal–epihyal juncture smooth, space between bones cartilage-filled; bone weakly interdigitating dorsally in large specimens of one observed species (Fig. 3). Hypohyals separated by wide, cartilage-filled space. Interhyal ventral surface with concave fossa; dorsal tip not greatly sculptured. Six branchiostegal rays present (except in *P. rima*), with four articulating with ceratohyal and two with epihyal. Urohyal large and broad, with well developed fossae dorsally for attachment of sternohyoideus muscle.

Ceratobranchial five (lower pharyngeals) dentigerous, unfused. Three pairs of ossified infra-pharyngobranchials (upper pharyngeals), associated with gill arches 2–4. Three ossified basibranchials; fourth an irregular cartilaginous pad. Uncinate processes on epibranchials three and four only. Gill rakers present on epibranchials, ceratobranchials, and usually one or two on hypobranchials, numbering 10–21 on first arch.

Posttemporal ventral ramus weak or absent (Fig. 4). Supracleithrum with thin, poorly ossified posterior lamina; median ridge well developed. Scapular foramen enclosed by bone; scap-

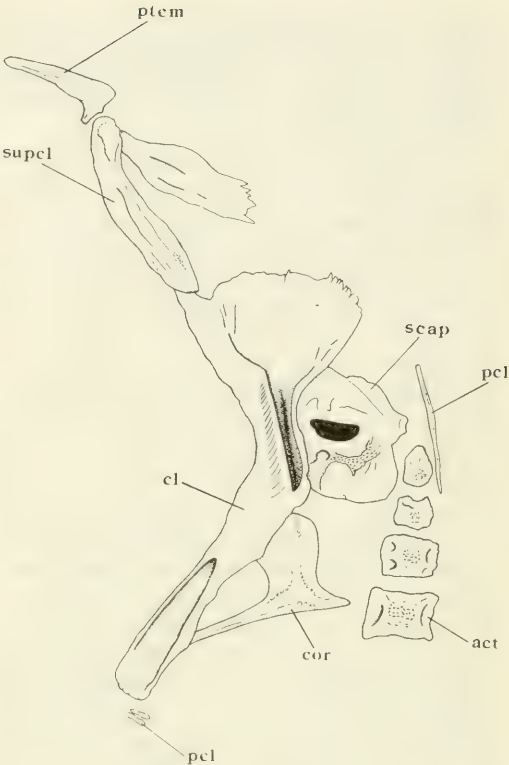


FIGURE 4. Left pectoral girdle of *Pachycara bulbiceps*, CAS 61220, 445 mm SL; lateral view. Pelvic bones greatly reduced in size in this species.

ula with well developed posterior strut. Four actinosts present bearing all pectoral rays but dorsalmost 2–3 (borne by scapular strut). Pelvic fins absent (*P. bulbiceps*), present (10 species), or variably present and absent (*P. mesoporum* and *P. sulaki*), with three (rarely two) soft rays. Single, needlelike postcleithrum present. Cleithrum with deep dorsal and ventral grooves for muscle attachments.

Vertebrae symmetrical. Epipleural ribs on vertebrae 1–21 or 22. Pleural ribs on third to ultimate precaudal vertebrae. Dorsal fin origin associated with vertebrae 2–8, with no free dorsal pterygiophores. First, or first and second, dorsal element a “flexible spine” (unsegmented and unbranched, but bilaterally divided at base); occasionally branched at tip, but this may be a preservation artifact. Last dorsal ray associated with second through fifth (usually fourth) preural vertebrae. Anal fin origin associated with antepenultimate to ultimate precaudal vertebrae, with 1–9 anal pterygiophores (all bearing soft rays)

inserted anterior to haemal spine of first caudal vertebrae. Last anal ray associated with second (rarely third) preural vertebrae. Caudal fin with 1–3 epural and 3–6 upper and lower hypural rays, totaling 8–12 rays.

COMPARATIVE REMARKS.—Recently, Arnulf et al. (1987) elaborated on the osteology and relationships of *Thermarces* Rosenblatt and Cohen, 1986, thought to be derived from *Pachycara* by the latter authors. *Thermarces* was diagnosed by Rosenblatt and Cohen, in part, on the basis of four characters shown by Arnulf et al. (1987) to have different states than those originally described (those of original description given first): (1) one or two suborbital ossifications vs. six; (2) pectoral radials unossified vs. ossified; (3) two pairs of infrapharyngobranchials vs. three; and (4) postcleithrum absent vs. present. The specimen of *Thermarces cerberus* (SIO 82-46) studied by Rosenblatt and Cohen was poorly ossified and I have observed, on subsequent restaining, a postcleithrum, six suborbital bones, four pectoral radials, and a cartilaginous third pharyngeal tooth plate. These structures, although bony, picked up very little or no alizarin-red stain, however. The skeletons of many deep-sea zoarcids are relatively unossified (Anderson and Hubbs 1981) and endochondral bone may not fully ossify in individuals of some species living in possibly environmentally stressful habitats. Stresses to normal calcium metabolism in the hydrothermal vent habitat of *Thermarces* may include high dissolved sulphide and metal ion levels (J. M. Edmonds, Massachusetts Institute of Technology, pers. comm.), making alizarin staining difficult (Anderson 1984). This seems to have been the case with the specimen cleared and stained by Rosenblatt and Cohen (1986) for illustration.

On the basis of the detailed osteology presented by Arnulf et al. (1987) and my studies, *Thermarces* does appear to be derived from, and very close to, *Pachycara*, although Arnulf et al. suggested *Thermarces* might be placed in a new subfamily someday. However, *Thermarces* is separable from *Pachycara* by only four characters: (1) pelvic bone absent; (2) scales absent; (3) lateral line absent; (4) flesh gelatinous. Although Arnulf et al. presented a detailed osteological description of *Thermarces*, their discussion on relationships and characters is flawed. For example, their table 1 is a very limited assemblage of

essentially non-diagnostic characters of higher groups, some of which are redundant. Their subfamily “Brotulinae” refers to the Parabrotulidae (Nielsen 1973, 1986; Anderson 1986). Subfamily Neozoarcinae was placed in Stichaeidae by Anderson (1984). *Melanostigma* was shown not to possess a basisphenoid bone by Anderson and Hubbs (1981). The attribution and interpretation of many characters of zoarcids by Arnulf et al. are mostly incorrect and a detailed discussion of these and an osteological analysis will be presented elsewhere.

KEY TO SPECIES OF *PACHYCARA*

- 1A. Branchiostegal rays six; pseudobranch present 2
- 1B. Branchiostegal rays four or five; pseudobranch absent *Pachycara rimae* n. sp.
Galapagos Rift Zone
- 2A. Occipital (supratemporal) pores absent (rarely present in *P. crossacanthum*; pre-caudal vertebrae 26–28 3
- 2B. Single, mesial occipital pore present; pre-caudal vertebrae 24–26
..... *Pachycara mesoporum* n. sp.
Peru and Chile
- 3A. Lateral line with mediolateral and ventral branches*; pre-caudal vertebrae 23–32; dorsal fin origin associated with vertebrae 3–8; anal fin origin associated with vertebrae 23–31 4
- 3B. Lateral line of ventral branch only; pre-caudal vertebrae 21–23; dorsal fin origin associated with vertebrae 2–3; anal fin origin associated with vertebrae 20–22
..... *Pachycara suspectum* (Garman, 1899)
Eastern Tropical Pacific
- 4A. Dorsal fin origin associated with vertebrae 3–7; pre-caudal vertebrae 23–30; head length 11.8–19.9% SL 5
- 4B. Dorsal fin origin associated with vertebra 8; pre-caudal vertebrae 32; head length 11.4% SL
..... *Pachycara shcherbachevi* n. sp.
Indian Ocean
- 5A. Gill rakers on lower limb (ceratobranchial) of first arch blunt, triangular 6

* Lateral line condition unknown in *P. shcherbachevi* n. sp.



FIGURE 5. Distribution of selected *Pachycara* species. Circles: *P. bulbiceps*; squares: *P. crassiceps*; hexagons: *P. crossacanthum*; triangles: *P. sulaki*; star: *P. shcherbachevi*.

- 5B. Gill rakers on lower limb of first arch bi- or tricuspid *Pachycara crossacanthum* n. sp.
Eastern Tropical Atlantic
- 6A. Origin of ventral branch of lateral line just posterior to last postorbital pore 7
- 6B. Origin of ventral branch of lateral line on or behind vertical through posterior third of pectoral fin *Pachycara sulaki* n. sp.
Western Tropical Atlantic
- 7A. Pelvic fins present 8
- 7B. Pelvic fins absent *Pachycara bulbiceps* (Garman, 1899)
NE Pacific and N Atlantic
- 8A. Suborbital pores along ventral ramus (beneath eye) six 9
- 8B. Suborbital pores beneath eye five *Pachycara brachycephalum* (Pappenheim, 1912)
Antarctica
- 9A. Origin of mediolateral branch of lateral line on or behind vertical through pectoral axil 10
- 9B. Origin of mediolateral branch of lateral line on nape, just posterodorsal to last postorbital pore *Pachycara pammelas* n. sp.
Chile
- 10A. Precaudal vertebrae 27–31 origin of mediolateral branch of lateral line anterior to vertical through posterior third of pectoral fin 11
- 10B. Precaudal vertebrae 23–26; origin of mediolateral lateral line at or posterior to vertical through posterior margin of pectoral fin *Pachycara lepinium*
Anderson and Peden, 1988
Northeastern Pacific
- 11A. Total vertebrae 102–109; caudal vertebrae 73–80; D 96–103; A 77–84; pectoral fin length 63.0–70.8% HL *Pachycara gymninium*
Anderson and Peden, 1988
Northeastern Pacific
- 11B. Total vertebrae 111–118; caudal vertebrae 84–88; D 105–112; A 86–92; pectoral fin length 81.6–97.0% HL *Pachycara crassiceps* (Roule, 1916)
Eastern Atlantic
- Pachycara bulbiceps* (Garman, 1899)**
(Figs. 1, 4, 5)
- Maynea bulbiceps* Garman, 1899:140–141, pl. E, fig. 1 (original description. Type locality: Gulf of Panama). McAllister and Rees, 1964:106, 107. Percy et al., 1982:387, 399, 400.
- Pachycara obesa* Zugmayer, 1911a:12; 1911b:134–136, pl. VI, fig. 6 (type locality: Bay of Biscay). Markle and Sedberry,

1978:22–25, fig. 1. Merrett and Marshall, 1981:240. Andriashev, 1973:547. Haedrich and Merrett, 1988:1335, 1338 (as *obesum*).

Pachycara obesa Zugmayer (lapsus calami). Fowler, 1936: 1056, fig. 437. Andriashev, 1986:1149, text fig.

Pachycara bulbiceps (Garman). Anderson and Peden, 1988: 84–88, figs. 1–3.

MATERIAL EXAMINED.—See Anderson and Peden (1988:84–85).

DIAGNOSIS.—Pelvic fins absent; mediolateral lateral line originating posterior to pectoral fin margin; scales absent on nape; vertebrae 25–31 + 82–91 = 112–119; D 104–114; A 86–97; P₁ 16–19; dorsal fin origin associated with vertebrae 4–7; gill rakers 0–4 + 11–15 = 11–19; branchiostegal rays six; suborbital pores 6–7; postorbital pores 1–3; head length 11.8–15.0% SL; pectoral fin length 8.7–12.9% SL.

DISTRIBUTION.—Both sides of the North Atlantic at depths of 2,400–4,780 m and in the northeastern Pacific from the Queen Charlotte Islands, Canada, to the Gulf of Panama at depths of 2,601–4,000 m (Fig. 5).

Pachycara crassiceps (Roule, 1916)

(Figs. 5, 6)

Lycenchelys crassiceps Roule, 1916:16 (original description).

Type locality: Bay of Biscay; based on two syntypes apparently lost).

Lycodes macrops (non Günther 1880). Vaillant, 1888:306–309.

Lycodes mucosus (non Richardson 1855). Vaillant, 1888:311–312.

Lycenchelys crassiceps. Roule, 1919:64–66, pl. V, fig. 1. Merrett and Marshall, 1981:240.

Lycodes sp. Golovan', 1974:289.

Lycodes atlanticus (non Jensen 1902). Golovan', 1978:226.

Lycodes crassiceps. Andriashev, 1986:1137, text fig.

MATERIAL EXAMINED.—BMNH 1981.6.23:3 (448 mm); Porcupine Sea Bight, SW of Ireland (51°14.7'N, 13°16.3'W); CHALLENGER sta. 50509; trawl, 1,490–1,523 m; 3 June 1979. ZIN 45347 (415 mm); off Cabo Barbas, Western (Spanish) Sahara (22°20'N, 17°30'W); ZVEZDA KRYMA sta. 260; trawl, 1,540–1,620 m; 16 Feb. 1973. BMNH 1981.6.23:1, 2 (432–518 mm); off Cap Blanc, Mauritania (20°09.1'N, 18°08.8'W); DISCOVERY sta. 9133-7; trawl, 2,130–2,191 m; 26 Nov. 1976. CAS 55587 (337 mm); off Senegal (13°12.5'N, 17°43.4'W); L. AMARO; trap, 1,300 m; 10 Feb. 1983. ZIN 45348 (509 mm); off Cape Fria, Namibia (18°26'S, 14°06'E); EVRIKA; trawl, 1,100–1,125 m; 22 Dec. 1975. IIPB 168/1985 (513 mm); off Namibia (23°05'S, 12°41'E); BENGUELA VII sta. 2; trawl, 652 m; 9 Aug. 1984. PEM 13784 (395 mm); off Cape of Good Hope, South Africa (33°40.0'S, 17°25.8'E); AFRICANA cruise 060, sta. A6999-01-04B; trawl, 923 m; 5 Mar. 1988. SAM uncat. (396 mm) off Cape of Good Hope (34°54.9'S, 18°12.1'E); AFRICANA cruise 060, sta. A7038-16-04B; trawl, 917 m; 14 Mar. 1988. SAM 31601 (189 mm); off Cape of Good Hope (33°37.5'S, 17°24.5'E); AFRICANA cruise 060, sta. A7002-

06-03B; trawl, 668 m; 8 Mar. 1988. RUSI 28210 (380 mm); off Cape of Good Hope (34°25.6'S, 17°41.2'E); AFRICANA sta. A4310; trawl, 760 m; 7 July 1986.

COUNTS AND MEASUREMENTS.—Vertebrae 27–30 + 84–90 = 111–118; D 105–112; A 86–94; C 10–12; P₁ 17–19; P₂ 3; vomerine teeth 6–8; palatine teeth 8–17; gill rakers 3 + 12–13; branchiostegal rays six; pseudobranch filaments 4–5. Following measurements in percent SL: head length 12.6–14.5; head width 8.0–10.3; pectoral fin length 10.7–13.3; predorsal length 17.3–21.6; preanal length 38.1–43.7; body height 10.7–13.6; gill slit length 5.5–7.4; caudal fin length 2.3–4.6. Following measurements in percent HL: head width 59.4–70.7; upper jaw length 38.7–45.4; pectoral fin length 81.6–97.0; snout length 17.4–23.4; eye diameter 17.3–20.8; gill slit length 40.4–50.7; interorbital width 8.5–11.4; interpupillary width 25.4–33.3; pelvic fin length 9.9–18.6 Pectoral base/length ratio 32.8–44.3.

DIAGNOSIS.—Pelvic fins present; mediolateral lateral line originating above pectoral fin just posterior to pectoral base; scales present on nape; vertebrae 27–30 + 84–90 = 111–118; gill rakers 15–21; pectoral fin length 81.6–97.0% HL.

DESCRIPTION.—Head ovoid, dorsal profile of snout more steeply sloping in large adults than juveniles. Scales extending anteriorly onto nape to about two eye diameters behind posterior margin of eye in large specimens; scales present on abdomen to isthmus, pectoral base and axil, and extending onto pectoral fin up to about half its length; scales present on unpaired fins almost to their margin. Eye circular, entering dorsal profile of head in large specimens. Gill slit extending to ventral margin of pectoral base. Lobe at dorsal margin of gill slit not formed in some large specimens; weak and rounded in juveniles. Pectoral fin origin at or slightly below body midline, insertion on abdomen; posterior margin of fin wedge-shaped (cf. *Lycodes*), pectoral rays 4–8 longest; ventralmost three or four rays thickened, tips slightly exserted.

Mouth subterminal, slightly oblique, upper jaw extending posteriorly to middle of eye. No epidermal prickles evident on snout or lips. Oral valve reaching anterior edge of vomer and coalesced with lateral margin of plate opposite vomer. Jaw teeth small, conical; dentary with 4–5 irregular rows anteriorly, blending into single posterior row; premaxilla with 3–4 anterior rows, blending into single posterior row. Vomerine teeth in irregular patch, longer and sharper in juveniles

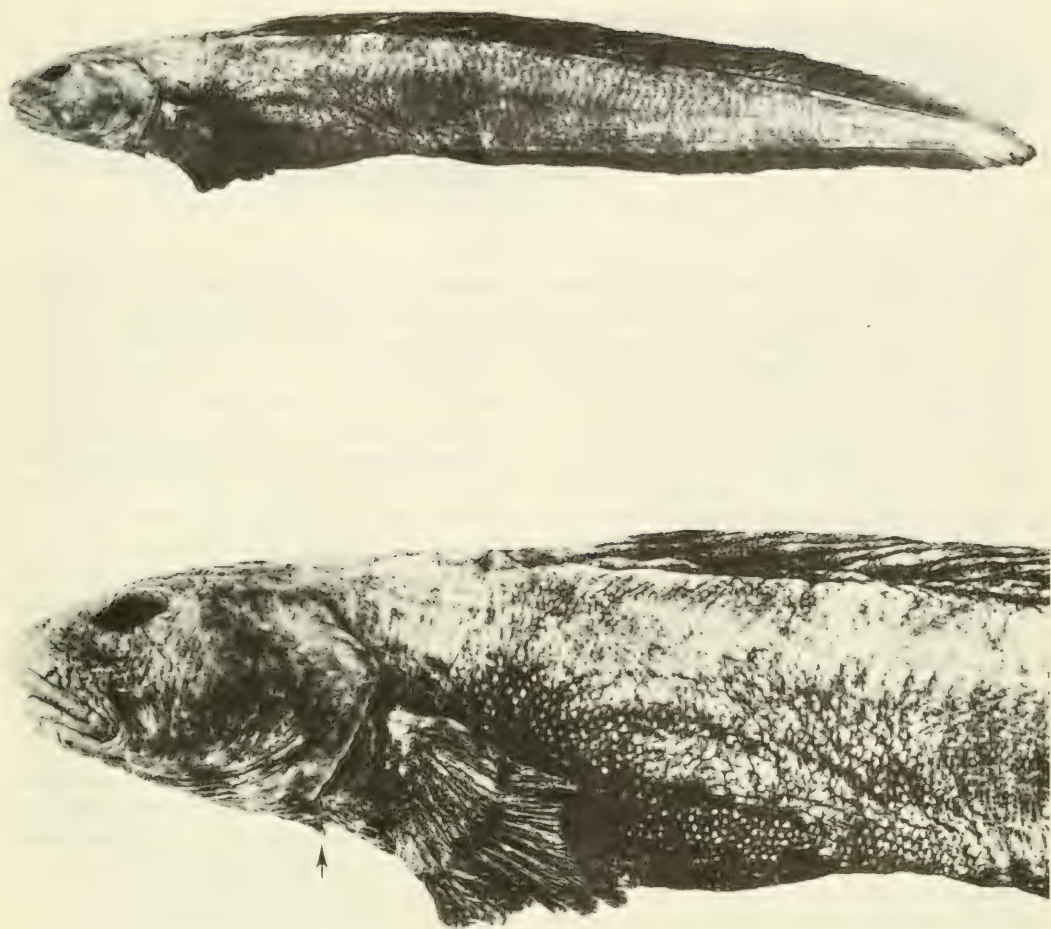


FIGURE 6. *Pachycara crassiceps* (Roule), BMNH 1981.6.23:1-2, 518 m SL, from off Cap Blanc, Mauritania. Arrow indicates pelvic fins.

than adults. Palatine teeth not retrorse, in double row at least anteriorly, in all.

Cephalic lateralis system with two or three postorbital pores (pores one and four, arising from frontal and lateral extrascapular, or pores one, three, and four). Two pairs of anterior supraorbital (nasal) pores, one set mesial to nasal tube, the other posteriorly. Six or seven suborbital pores, six arising from ventral ramus of bone chain and one (absent in three specimens; absent on one side only in one specimen) from ascending ramus behind eye just ventral to first postorbital pore. Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular, and three from preopercle. Interorbital and occipital pores absent. Body lateral line system with mediolateral branch originating above pec-

toral fin about one eye diameter posterior to pectoral base; ventral branch originating just posterior to fourth postorbital pore; both branches complete to tail tip. Free superficial neuromasts (about 8-10) forming dorsal "lateral line" originating above pectoral base on horizontal through middle of eye and extending posteriorly to vertical through posterior margin of pectoral fin or slightly anteriorly.

Dorsal fin origin associated with vertebrae five or six. Anal fin origin associated with ultimate precaudal vertebrae (numbers 25-30), with 3-5 anal pterygiophores inserted anterior to haemal spine of first caudal vertebra. Last dorsal ray associated with fourth preural vertebra, last anal ray associated with second preural vertebra. Caudal fin with two epural, 4-5 upper and 4-5 lower

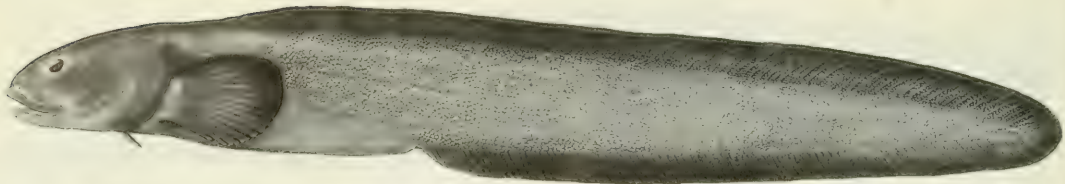


FIGURE 7. *Pachycara crossacanthum* n. sp., CAS 62408, paratype, 227 mm SL, from off Senegal.

hypural rays. Gill rakers, small, dorsalmost on lower limb (ceratobranchial) triangular, sharply pointed, ventralmost blunt; ventralmost four rakers in ZIN 45347 with tricuspid tips. Branchiostegal rays six. Pseudobranch filaments long, simple.

Color uniformly black (adults) or dark chocolate brown (juveniles), in recently preserved material. Eye blue. Abdomen with bluish tinge in juveniles, black in adults. Lining of orobranchial cavity black, lateral regions of palate pale.

DISTRIBUTION.—Known in eastern Atlantic from SW of Ireland to off South Africa on upper and lower continental slopes at depths of 652–2,191 m (Fig. 5).

REMARKS.—This species was originally described from two syntypes, neither of which were found. However, a neotype is not selected here as the syntypes have not been sufficiently searched for, and diagnostic features (counts of the axial skeleton from x-radiography) published in Roule (1919) permit the distinction of *P. crassiceps* from its close congener, *P. crossacanthum* (below). Pectoral fin ray counts in Roule (1919) are, however, undoubtedly erroneous.

Pachycara crossacanthum n. sp.

(Figs. 5, 7, 8)

HOLOTYPE.—CAS 55586 (female, 370 mm); off Senegal (12°58.0'N, 17°41.8'W); L. AMARO sta. Casamance; fish trap, 900 m; B. Seret, 8 Feb. 1983.

PARATYPES.—MNHN 1988-1170 (3; 227–378 mm); collected with holotype. CAS 62408 (female, 227 mm); off Senegal (15°47.8'N, 17°07.1'W); L. AMARO, sta. 6; fish trap, 900 m; D. Gaertner, 29 Mar. 1984. MNHN 1988-1169 (female, 353 mm); off Pointe Banda, Gabon (04°00'S, 10°08'E); NIZERY sta. 14-76; fish trap, 1,050 m; A. Crosnier, 20 May 1976.

COUNTS AND MEASUREMENTS.—Vertebrae 26–28 + 75–79 = 101–107; D 97–103; A 77–83; C 10–12 P₁ 17–18; P₂ 3; vomerine teeth 5–14; palatine teeth 6–16; gill rakers 3 + 12–13; branchiostegal rays six; pseudobranch filaments 4–5. Following measurements in percent SL: head length 14.8–16.9; head width 8.6–9.5; pectoral

fin length 9.2–10.5; predorsal length 17.6–19.7; preanal length 41.3–44.2; body height 9.6–11.8; gill slit length 5.8–6.7; caudal fin length 3.4–5.0. Following measurements in percent HL: head width 52.7–64.5; upper jaw length 35.5–45.6; pectoral fin length 54.6–66.0; snout length 19.1–23.2; eye diameter 15.2–20.2; gill slit length 34.9–41.8; interorbital width 6.9–10.3; interpupillary width 21.1–25.3; pelvic fin length 12.2–18.0. Pectoral base/length ratio 38.9–50.9.

DIAGNOSIS.—Pelvic fins present; dorsal gill rakers on first arch bi- or tricuspid at tips (adults and subadults); scales absent on nape and abdomen; postorbital pores four; vertebrae 26–28 + 75–79 = 101–107; origin of mediolateral lateral line near dorsal margin of pectoral base; occipital pores present or absent.

DESCRIPTION.—Head ovoid, snout not bluntly rounded (as some species), but steep anteriorly. Scales extending anteriorly on body in wedge-shaped pattern to vertical from half pectoral fin

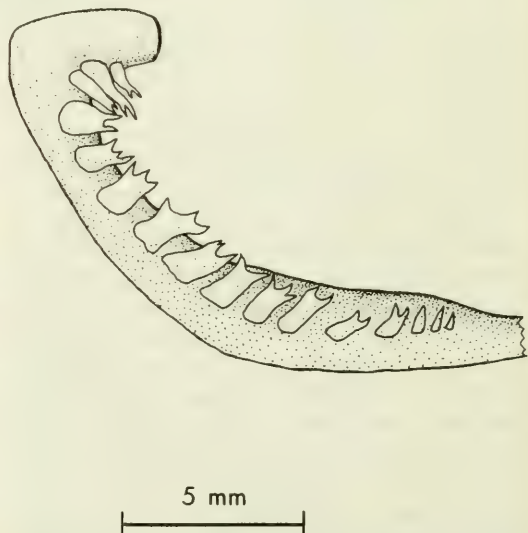


FIGURE 8. Outer surface of right first gill arch of holotype of *Pachycara crossacanthum* n. sp., showing furcated gill rakers; gill lamellae not shown.

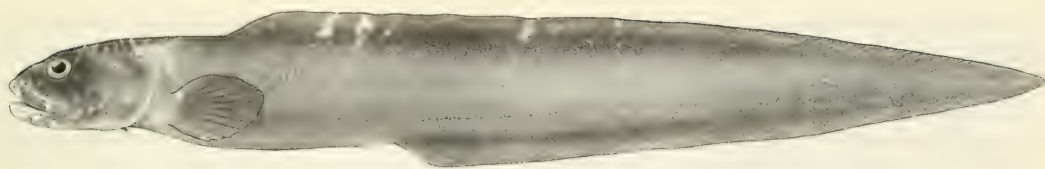


FIGURE 9. *Pachycara sulaki* n. sp., USNM 292811, holotype, 189 mm SL, from off Puerto Rico.

length posterior to pectoral margin (usually in smallest specimens) to vertical through middle of pectoral; scales absent on abdomen, nape, pectoral axil and base. Eye ovoid, entering dorsal profile of head. Gill slit short, not reaching ventral margin of pectoral base. Lobe at dorsal margin of gill slit rounded and weakly developed in three specimens (including holotype), squared-off and well defined in others. Pectoral fin origin well below body midline, insertion on abdomen; posterior margin of fin evenly rounded, middle rays longest; ventralmost four or five rays thickened, tips slightly exserted.

Mouth subterminal, oblique, upper jaw extending posteriorly to middle of eye, or slightly in advance. No epidermal prickles evident on snout or lips. Oral valve weak, not reaching anterior edge of vomer, and not coalesced with lateral margin of palate opposite vomer. Jaw teeth in large specimens long, sharp, retrorse anteriorly; dentary with 4–5 irregular rows anteriorly, blending into single posterior row; premaxilla with two (males) or three (females) anterior rows, blending into single posterior row. Vomerine teeth in irregular patch; palatine teeth not retrorse, in double row in large females, in single row in all others.

Cephalic lateralis system with four postorbital pores arising from frontal (pore one), pterotic (pore two), between pterotic and lateral extrascapular (pore three) and just posterior to lateral extrascapular (pore four). Two pairs of anterior supraorbital (nasal) pores, one set mesial to nasal tube, the other posteriorly. Seven suborbital pores, six arising from ventral ramus of bone chain and one from ascending ramus behind eye just ventral to first postorbital pore. Eight preoperculo-mandibular pores, four arising from dentary, one from anguloarticular and three from preopercle. Interorbital and occipital pores absent, except in CAS 62408 which has three minute occipital pores and MNHN 1988-1170, 227 mm SL, which has a single, right lateral occipital pore. Body lateral line with mediolateral branch

originating in pectoral axil near dorsal margin of pectoral base; ventral branch originating just posterior to fourth postorbital pore; both branches complete to tail tip.

Dorsal fin origin associated with vertebra four. Anal fin origin associated with ultimate precaudal vertebra (numbers 26–28), with three anal pterygiophores inserted anterior to haemal spine of first caudal vertebra. Last dorsal ray associated with fourth preural vertebra, last anal ray associated with second preural vertebra. Caudal fin with 1–2 epural, 4–5 upper and 4–6 lower hypural rays.

Gill rakers on upper limb (epibranchial) of first arch long, sharply pointed in young, bi- or trifurcate in large specimens; rakers on lower limb (ceratobranchial) tubular, those of large specimens with bi- or tricuspid tips (Fig. 8); lowermost 1–4 rakers of some specimens simple, pointed. Branchiostegal rays six. Pseudobranch filaments 4–5, tips furcate in large specimens.

Color uniformly dark brown, margins of dorsal, anal and pectoral fins black; eye and abdomen bluish. Peritoneum and inner palate black. Lips and lining of lateral sides of palate white.

DISTRIBUTION.—Known off western tropical Africa from Senegal to Gabon on the upper continental slope at depths of 900–1,050 m (Fig. 5).

ETYMOLOGY.—From the Greek *κρόσσος* (fringe) and *ἄκανθα* (thorn) in reference to the species' furcate gill rakers.

Pachycara sulaki n. sp.

(Figs. 5, 9)

Zoarcid fish. Paull et al., 1984:965, 966.

Pachycara sp. Anderson et al., 1986:800.

HOLOTYPE.—USNM 292811 (male, 189 mm); Mona Passage off Puerto Rico (18°28.7'N, 67°20.6'W); PEZMAR, Deep Trapping Project, sta. 36; medium fish trap, 2,000 m; D. A. Hensley, 12–13 Feb. 1986.

PARATYPES.—USNM 233627 (female, 161 mm); Venezuela Basin, Caribbean Sea (13°31.3–25.7'N, 64°45.1–40.4'W); USNS BARTLETT sta. E092; trawl, 3,510–3,469 m; M. D. Richardson and party, 28 Nov. 1981. SIO 87-33 (female, 133 mm);

Florida Escarpment, Gulf of Mexico (26°05'N, 84°54'W); DSV ALVIN dive 1771; Floc Sucker, 3,303 m; C. Paull and party, 7 Nov. 1986.

COUNTS AND MEASUREMENTS.—Vertebrae 27–30 + 80–85 = 107–113; D 99–107; A 81–89; C 9–11; P₁ 16–17; P₂ 0 or 3; vomerine teeth 4–8; palatine teeth 4–7; gill rakers 2–3 + 9–13 = 11–16; branchiostegal rays six; pseudobranch filaments 3–4. Following measurements in percent SL: head length 14.8–17.7; head width 7.3–9.0; pectoral fin length 9.8–10.6; predorsal length 20.8–23.5; preanal length 39.0–41.7; body height 8.3–9.5; gill slit length 4.8–6.5; caudal fin length 2.1–3.8. Following measurements in percent HL: head width 47.8–56.1; upper jaw length 36.4–50.0; pectoral fin length 55.5–68.8; snout length 16.4–20.1; eye diameter 17.8–23.9; gill slit length 28.0–42.1; interorbital width 6.4–10.5; interopercular width 23.8–32.8; pelvic fin length 5.7–13.9 (in two). Pectoral base/length ratio 38.9–40.0.

DIAGNOSIS.—Pelvic fins present or absent; origin of mediolateral lateral line just posterior to last (fourth) postorbital pore; origin of ventral lateral line on or behind vertical through posterior third of pectoral fin; suborbital pores 5–6; dorsal fin origin associated with vertebrae 6–7; vertebrae 27–30 + 80–85 = 107–111; predorsal length 20.8–23.5% SL.

DESCRIPTION.—Head ovoid, long, dorsal profile evenly tapering; snout bluntly rounded. Scales extending anteriorly on body in wedge-shaped pattern to vertical through middle of pectoral fin (all three specimens juveniles; adults probably more densely scaled); scales absent in these juveniles on dorsal fin anteriorly (present on posterior third), abdomen, head, nape, pectoral base and axil. Eye circular, entering dorsal profile of head. Gill slit reaching ventral margin of pectoral base or just above it. Lobe at dorsal margin of gill slit weak, rounded. Pectoral fin origin just below body midline, insertion on abdomen; posterior margin of fin evenly rounded, middle rays longest; ventralmost five rays thickened, tips slightly exerted. Pelvic fins present except in SIO 87-33; of three soft rays each in other two specimens.

Mouth subterminal, oblique, upper jaw extending posteriorly to middle of eye in females (paratypes), or its rear margin in male holotype. No epidermal prickles evident on snout or lips. Oral valve well developed in these small speci-

mens, overlapping anterior edge of vomer and not coalesced with lateral margins of plate opposite vomer. Jaw teeth relatively long and sharp in male, smaller and conical in females; outer jaw teeth retrorse; both jaws (all specimens) with two irregular rows of teeth blending into single, posterior row. Vomerine teeth in irregular patch, enlarged in male; palatine teeth not retrorse, in single row.

Cephalic lateralis system with two postorbital pores arising from frontal (pore one) and lateral extrascapulars (pore four). Two pairs of anterior supraorbital (nasal) pores, one set mesial to nasal tube, the other posteriorly. Five (USNM 233627) or six suborbital pores, all arising from ventral ramus of bone chain. Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle. Interorbital and occipital pores absent. Superficial neuromasts prominent on head an anterior portion of body, with series on preopercle, behind eye running along occiput in converging row, around rictus of mouth, and snout between nostrils. Body lateral line with mediolateral branch originating just behind posteriormost (number four) postorbital pore; this branch undulating across body somewhat, then straightening above anus; ventral branch originating on or slightly behind (holotype) posterior third of pectoral fin; both branches complete to tail tip.

Dorsal fin origin associated with vertebrae 6–7. Anal fin origin associated with penultimate or ultimate precaudal vertebrae (numbers 26–30), with 3–5 anal pterygiophores inserted anterior to haemal spine of first caudal vertebra. Last dorsal ray associated with fourth preural vertebra, last anal ray associated with second preural vertebra. Caudal fin with two epural, 3–5 upper hypural and four lower hypural rays.

Gill rakers on upper limb (epibranchial) and dorsalmost rakers on lower limb (ceratobranchial) narrow and sharply pointed; ventralmost ceratobranchial rakers blunt, triangular. Branchiostegal rays six. Pseudobranch filaments long, numbering 3–4.

Live color notes or photographs of all three specimens available, each one quite different. Holotype uniformly dark chocolate brown, as most other congeners, unpaired fins black, eye blue. Paratype USNM 233627 from the Caribbean Sea with lustrous dark blue body, typical of many deep-sea fishes such as halosaurs and

alepocephalids (Markle 1980, fig. 1), head and pectoral fins black. Paratype SIO 87-33 relatively blanched, body uniformly sandy gray, occiput, nape and pectoral axil occupied by a wide, white band, eye and abdomen blue, unpaired fins translucent.

DISTRIBUTION.—Known only from three specimens taken in abyssal waters of the tropical northwestern Atlantic at depths of 2,000–3,510 m (Fig. 5).

ETYMOLOGY.—Named after Kenneth J. Sulak, intrepid explorer of the great murky depths of the Atlantic Ocean, to honor his many contributions to knowledge of the deep-sea fishes of this and adjacent regions.

***Pachycara shcherbachevi* n. sp.**

(Figs. 5, 10)

HOLOTYPE.—ZMUC P-761147 (female, 236 mm SL); Bay of Bengal (15°54.0'N, 90°17.0'E); GALATHEA sta. 314; trawl (HOT/4800), 2,600 m; 1930 hr; 3 May 1951.

COUNTS AND MEASUREMENTS.—Vertebrae 32 + 90 = 122; D 112; A 94; C 12; P₁ 17; P₂ 3; vomerine teeth two; palatine teeth 4/4; gill rakers 2 + 14; branchiostegal rays six; pseudobranch filaments three. Following measurements in percent SL: head length 11.4; head width 7.7; pectoral fin length 10.0; predorsal length 16.6; preanal length not measurable; body height 7.7; caudal fin length 3.0. Following measurements in percent HL: head width 67.7; upper jaw length 39.0; pectoral fin length 87.7; snout length 16.0; eye diameter 23.8; interorbital width 13.8; interopillary width 28.6; pelvic fin length 8.9. Pectoral base/length ratio 36.0.

DIAGNOSIS.—Pelvic fins present; vertebrae 32 + 90 = 122; dorsal fin origin associated with vertebra eight; head length 11.4% SL.

DESCRIPTION.—Specimen trawl damaged—completely skinned, body torn before anus; scales, lateral line, and most head pores not evident. Head ovoid, small; its length shorter in relation to SL than any *Pachycara* specimen, irregardless of size. Eye large, ovoid, entering dorsal profile of head when viewed laterally. Gill opening damaged, tissue covering branchiostegal membranes torn, but adhering on left side in places, and with skin along pectoral base, gill opening appearing to extend ventrally to just above lower pectoral base. Dorsal margin of gill slit with short, anteriorly directed emargination. Pectoral fin origin

well below body midline, insertion on abdomen; posterior margin of fin (from reconstruction utilizing both fins) evenly rounded, middle rays longest; ventralmost four rays thickened.

Mouth subterminal, upper jaw (premaxilla and maxilla with some flesh) posteriorly relatively high, somewhat rectangular. Oral valve reaching anterior edge of vomer and coalesced with lateral margin (left) of palate opposite vomer. Jaw teeth small, conical, retrorse anteriorly; dentary with 14 teeth in two irregular rows anteriorly, blending into single, posterior row; premaxillae with 13 (right) or 11 (left) teeth, also in two irregular rows anteriorly, blending into single, posterior row. Two small vomerine teeth. Four palatine teeth on both bones, in short row.

Cephalic lateralis pores evident from connective tissue tubules and impressions in exposed subdermal lipid layer, not all pores remaining. Presumably two pairs of anterior supraorbital pores mesial to nasal tube. Six suborbital pores, all arising from ventral ramus of bone chain under eye. Eight preoperculo-mandibular pores, four arising from dentary, one from anguloarticular, and three from preopercle. Interorbital and occipital pores presumably absent. Postorbital pores one (behind eye) and four (anterodorsal upper end of gill slit) observed, others (pore two and three) may or may not be present in the species.

Dorsal fin origin associated with vertebra eight; posteriormost origin in genus, except for *P. rimae*, n. sp., which also has dorsal origin with eighth vertebra. Anal fin origin associated with penultimate precaudal vertebra (number 31), with four anal pterygiophores inserted anterior to haemal spine of first caudal vertebra. Last dorsal ray associated with fourth preural vertebra; last anal ray associated with second preural vertebra. Caudal fin with two epural, five upper hypural, and five lower hypural rays.

Gill rakers small, sharply pointed and pyramidal dorsally; ventralmost five much smaller than dorsalmost, but distinct. Branchiostegal rays six. Pseudobranch filaments three, very small.

Color unknown, but bits of black skin adhere to head, body, and fins. Perhaps all black in life. Peritoneum black. Lining of orobranchial chamber dark brown in alcohol, probably black in life also.

DISTRIBUTION.—Known from a single specimen from the abyssal Bay of Bengal, northwest of the Andaman Islands, in 2,600 m (Fig. 5).



FIGURE 10. *Pachycara shcherbachevi* n. sp., ZMUC P-761147, holotype, 236 mm SL, Bay of Bengal (specimen damaged by trawl).

ETYMOLOGY.—Named after Yuri Nikolaevich Shcherbachev, P. P. Shirshov Institute of Oceanology, Academy of Sciences, USSR, friend and colleague, in honor of his pioneering contributions to knowledge of the deep-sea fishes of the Indian Ocean.

***Pachycara gymninium* Anderson and Peden, 1988**
(Fig. 11)

Lycodes sp. Hubbs et al., 1979:14.

Lycenchelys "E." Percy et al., 1982:387.

Pachycara gymninium Anderson and Peden, 1988:88–91, fig. 5.

MATERIAL EXAMINED.—See Anderson and Peden (1988:88–89).

DIAGNOSIS.—Pelvic fins present, their length 4.8–11.3% HL; mediolateral lateral line originating in pectoral axil just posterior to vertical through pectoral base; scales absent on nape, or, if present, not extending anterior to line connecting anterodorsal edges of gill slits; vertebrae 28–31 + 73–80 = 102–109; D 96–103; A 77–84; P₁ 14–18; dorsal fin origin associated with vertebrae 3–5; anal fin origin associated with vertebrae 27–31; gill rakers 3–5 + 10–14 = 13–19; branchiostegal rays six; suborbital pores 6–7; postorbital pores 2–3; head length 12.0–15.6% SL; pectoral fin length 63.0–70.8% HL.

DISTRIBUTION.—Eastern North Pacific off the Queen Charlotte Islands, Canada, south to the Gulf of California at depths of 1,829–3,225 m (Fig. 11).

***Pachycara lepinium* Anderson and Peden, 1988**
(Fig 11)

Lycodes sp. Hubbs et al., 1979:14.

Lycenchelys "D." Percy et al., 1982:387.

Pachycara lepinium Anderson and Peden, 1988:91–92, fig. 6.

MATERIAL EXAMINED.—See Anderson and Peden (1988:91).

DIAGNOSIS.—Pelvic fins present, their length 11.5–17.3% HL; mediolateral lateral line originating posterior to pectoral fin margin; scales present on nape; vertebrae 23–26 + 80–94 = 105–120; D 99–113; A 85–98; P₁ 15–18; dorsal fin origin associated with vertebrae 4–5; anal fin origin associated with vertebrae 23–26; gill rakers 2–5 + 11–15 = 12–19; branchiostegal rays six; suborbital pores six; postorbital pores 2–3; head length 13.8–15.9% SL; pectoral fin length 72.5–89.9% HL.

DISTRIBUTION.—Eastern North Pacific off the Queen Charlotte Islands, Canada, south to off Cabo Colnett, Baja California Norte, Mexico, at depths of 1,728–2,907 m (Fig. 11).

***Pachycara suspectum* (Garman, 1899)**
(Fig. 11)

Phucocoetes suspectus Garman, 1899:137, pl. XXX, figs. 3, 3a.
Pachycara suspectum (Garman). Anderson and Peden, 1988: 88, fig. 4.

MATERIAL EXAMINED.—See Anderson and Peden (1988:88).

DIAGNOSIS.—Pelvic fins present; lateral line of ventral branch only; scales absent on nape; vertebrae 21–23 + 84–87 = 105–110; D 100–106;

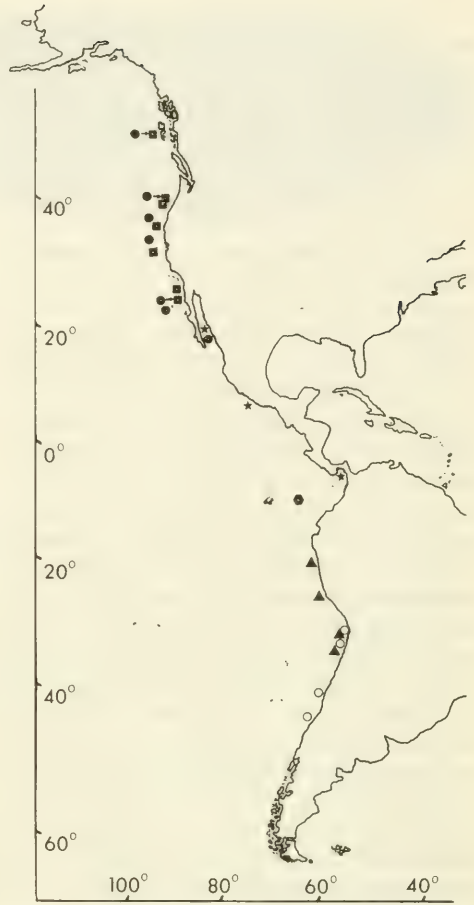


FIGURE 11. Distribution of eastern Pacific species of *Pachycara*. Closed circles: *P. gymninium*; squares: *P. lepinium*; hexagon: *P. rimae*; triangles: *P. mesoporum*; stars: *P. suspectum*; open circles: *P. pammelas*.

A 85–89; P₁ 16; dorsal fin origin associated with vertebrae 2–3; anal fin origin associated with vertebrae 20–22; gill rakers 1–2 + 14–15 = 16; branchiostegal rays six; suborbital pores seven; postorbital pores three; head length 15.6–17.7% SL; pectoral fin length 57.4–58.6% HL.

DISTRIBUTION.—Eastern North Pacific in the Gulf of California south to the Gulf of Panama at depths of 915–1,280 m (Fig. 11).

***Pachycara rimae* n. sp.**
(Figs. 11, 12)

Zoaridae (partim). Cohen and Haedrich, 1983:376.
Pachycara (?). Cohen et al., 1985:229.

HOLOTYPE.—LACM 44699-1 (male, 403 mm SL); vic. Galapagos Rift hydrothermal vents (00°47.8'N, 86°09.9'W); DSV ALVIN; baited trap, 2,500 m; J. Corliss, 16 Mar. 1977.

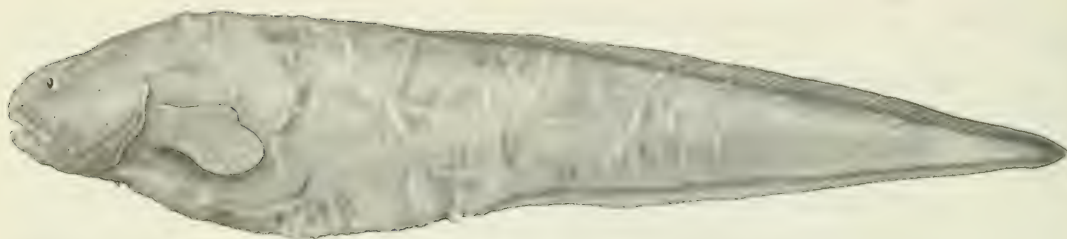


FIGURE 12. *Pachycara rimae* n. sp., LACM 44699-1, holotype, 403 mm SL, Galapagos Rift Zone. Illustration of right side shown in left lateral view (left side damaged).

COUNTS AND MEASUREMENTS.—Vertebrae 26 + 67 = 93; D 86; A 70; C 9; P₁ 15; P₂ 2; vomerine teeth three; palatine teeth 8–9; gill rakers 3 + 7; branchiostegal rays four or five; pseudobranch filaments absent. Following measurements in percent SL: head length 13.7; head width 10.1; pectoral fin length 9.3; predorsal length 21.6; preanal length 44.2; body height 14.1; gill slit length 6.0; caudal fin length 1.7. Following measurements in percent HL: head width 74.2; upper jaw length 54.3; pectoral fin length 68.1; snout length 18.9; eye diameter 13.0; gill slit length 43.7; interorbital width 12.7; interpupillary width 42.1; pelvic fin length 4.2. Pectoral base/length ratio 42.7.

DIAGNOSIS.—Pelvic fins nublike, of two soft rays; vertebrae 26 + 67 = 93; D 86; A 70; lateral line of mediolateral branch only; dorsal fin origin associated with vertebra eight; pseudobranch absent; branchiostegal rays four or five; suborbital pores five; gill rakers 10.

DESCRIPTION.—Head deep, rounded, somewhat shorter than similarly sized congeners. Snout steeply sloping anteriorly. Left side of body and tail damaged, but skin pliable around head and dorsum owing to subdermal lipid layer. Scales extending anteriorly on body in wedge-shape pattern to vertical just anterior to posterior margin of pectoral fin; scales absent on head, nape, dorsum, pectoral base, abdomen, and unpaired fins. Eye small, circular, entering dorsal profile of head when viewed laterally. Gill slit short, extending ventrally to opposite pectoral ray 12. Lobe at dorsal margin of gill slit weakly developed, gill slit not continued anteriorly. Pectoral fin origin well below body midline; left pectoral fin badly damaged in capture, right fin deformed, apparently injured in life, with tips of dorsalmost four rays missing (Fig. 12); six ventralmost pectoral rays thickened, slightly exserted at tips.

Mouth terminal, oblique, upper jaw extending

posteriorly to middle of eye or beyond (snout region twisted to one side). No epidermal prickles evident on snout or lips. Oral valve just reaching anterior margin of vomer and coalesced with lateral margins of palate opposite vomer. Teeth small, conical, sharp. Jaw teeth in double row anteriorly, blending into single, posterior row. Vomerine teeth three, in an arc; palatine teeth in single row.

Cephalic lateralis system with two postorbital pores arising from frontal (pore one) and lateral extrascapular (pore four). Two pairs of anterior supraorbital (nasal) pores, one set anteromesial to nasal tube, the other posteromesially. Five suborbital pores, all arising from ventral ramus of suborbital bone chain. Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular, and three from preopercle. Interorbital and occipital (supratemporal) pores absent. Body lateral line mediolateral, originating posterior to rear margin of pectoral fin, complete to tail tip; no ventral branch.

Dorsal fin origin associated with vertebra eight. Anal fin origin associated with ultimate precaudal vertebra (number 26), with two anal pterygiophores inserted anterior to haemal spine of first caudal vertebra. Last dorsal ray associated with fourth preural vertebra, last anal ray associated with second preural vertebra. Caudal fin with two epural, four upper hypural, and four lower hypural rays.

Gill rakers very short, triangular, lowermost rakers on first arch mere nubs; raker denticles absent. Branchiostegal rays four on right side (two articulating with ceratohyal, two with epihyal) and five on left side (three articulating with ceratohyal, two with epihyal). Pseudobranch absent.

Color uniformly light brown (Cohen et al. 1985: 229); eye and abdomen bluish. Peritoneum and lining of orobranchial chamber dark brown in alcohol, probably black in life. Head and right



FIGURE 13. *Pachycara mesoporum* n. sp., CAS 62406, holotype, 485 mm SL, from off Antofagasta, Chile.

pectoral fin with scattered whitish blotches and streaks.

DISTRIBUTION.—Known only from the holotype taken in the abyssal southeastern Pacific in 2,500 m.

ETYMOLOGY.—From the Latin “rima” (fissure). A genitive noun in apposition, alluding to the species’ capture at the Galapagos Rift Zone (Cohen and Haedrich 1983; Cohen et al. 1985).

***Pachycara mesoporum* n. sp.**

(Figs. 11, 13)

HOLOTYPE.—CAS 62406 (male, 485 mm); off Antofagasta, Chile; Chilean fisheries vessel; trawl, depth uncertain (ca. 300 m); I. Kong Urbina, 18 Apr. 1986.

PARATYPES.—LACM 43717-1 (5; 170–217 mm); off Trujillo, Peru (08°26'S, 80°36.5'W); ANTON BRUUN sta. 650E; free vehicle set line trap, 1,830 m; L. Knapp and party, 8–9 June 1966. ZIN 48394 (male, 189 mm); off Laguna Grande, Peru (14°44'S, 76°12'W); DMITRY MENDELEEV cr. 20, sta. 1654; Galathea trawl, 1,495–1,430 m; N. V. Parin, 2335–0120 hr, 19–20 Mar. 1978. MNHNC 6653 (female, 318 mm); off Arica, Chile (18°26'S, 70°37'W); TIBERIADES; trawl, 760 m; I. Kong Urbina, 17 Feb. 1981.

COUNTS AND MEASUREMENTS.—Vertebrae 24–26 + 78–87 = 103–113; D 96–108; A 80–90; C 9–10; P₁ 15–18; P₂ absent or three; vomerine teeth 3–12; palatine teeth 2–11; gill rakers 2–3 + 11–16 = 13–18; branchiostegal rays six; pseudobranch filaments 3–4. Following measurements in percent SL: head length 12.6–15.9; head width 6.1–8.2; pectoral fin length 8.8–12.1; predorsal length 15.1–18.1; preanal length 33.6–38.1; body height 7.8–9.5; gill slit length 4.1–6.9; caudal fin length 2.1–3.2. Following measurements in percent HL: head width 44.6–52.5; upper jaw length 34.7–51.7; pectoral fin length 57.1–81.1; snout length 16.0–21.2; eye diameter 17.2–22.9; gill slit length 28.1–44.3; interorbital width 5.9–9.0; interpupillary width 24.0–29.6; pelvic fin length 8.0–8.8 (in two of eight). Pectoral base/length ratio 32.8–46.3.

DIAGNOSIS.—Pelvic fins present or absent; single, mesial occipital pore present; postorbital

pores 3–4; mediolateral lateral line originating slightly anterior to vertical through posterior margin of pectoral fin; ventral lateral line originating just posterior to last postorbital pore; vertebrae 24–26 + 78–87 = 103–113.

DESCRIPTION.—Following description based on one adult male (holotype), one adult female (MNHNC 6653), three juvenile males, and three juvenile females. Head ovoid in juveniles and adult female, more triangular in adult male. Male with dorsoventrally depressed head and straighter snout than others; adult female and juveniles with bluntly rounded snouts. Scales extending anteriorly to vertical through dorsal fin origin, or slightly anterior to it; scales absent on nape (rare or absent anterior to line connecting upper edge of gill slit and dorsal fin origin). Scales present on unpaired fins (almost to their margin posteriorly), abdomen to isthmus, in pectoral axil and on pectoral base except adult female and one juvenile male. Eye ovoid, more rounded in adult male, entering dorsal profile of head except in adult female; eye diameter 17.2% HL in adult male, 20.2–22.9% HL in others. Gill slit short, not reaching ventral margin of pectoral base except in adult male, in which it reaches slightly beyond lowest pectoral ray; gill slit length 42.2% HL in male, 28.1–34.0% HL in juveniles, and 44.3% HL in adult female owing to its anterior extension (below). Lobe at dorsal margin of gill slit small, squared-off in holotype and some juveniles; dorsal margin not extending anteriorly in some juveniles; operculum broadly rounded and extending anteriorly almost one eye diameter in adult female. Pectoral fin origin on body midline in smallest juveniles, well below midline in adults, insertion on abdomen; posterior margin of fin usually evenly rounded, middle rays longest, however, female with left fin distinctly wedge-shaped and right fin injured, with tips of upper and middle rays missing (fin deeply notched). Ventralmost four or five pectoral rays thickened, tips slightly exerted.

Mouth subterminal, oblique, snout and upper jaw more produced in adult male than others; upper jaw extending posteriorly to rear margin of eye in adult male (upper jaw length 51.7% HL), or to middle of eye in others (37.1–42.1% HL in adult female and juveniles). No epidermal prickles evident on snout or lips. Oral valve weak, not reaching anterior edge of vomer in adults, but not coalesced with lateral margin of palate opposite vomer in any specimen. Jaw teeth in adult male long, caniniform, slightly retrorse (Fig. 13); dentary with three irregular rows anteriorly, blending into single, posterior row; premaxilla with two irregular anterior rows, blending into single, posterior row; outer row on premaxilla about five times as large as inner row. Jaw teeth in adult female and juveniles small, blunt, conical; dentary with four irregular rows anteriorly (juveniles with 2–3 rows), blending into single, posterior row; premaxilla with three irregular anterior rows (juveniles with two), blending into single, posterior row. Vomerine teeth in irregular patch or gradual arc (holotype). Vomerine and palatine teeth retrorse and caniniform in adult male, small, blunt and conical in others; palatine teeth in irregular, double row in adult female, in single row in others.

Cephalic lateralis system with three postorbital pores arising from frontal (pore one), between pterotic and lateral extrascapular (pore three), and just posterior to lateral extrascapular (pore four) except in adult female in which pore two is present on both sides, arising from pterotic. Two pairs of anterior supraorbital (nasal) pores, one set mesial to nasal tube, the other posteriorly (posteromesially in adult male). Usually seven suborbital pores, with six arising from ventral ramus of bone chain and one from ascending ramus behind eye. Exceptions to this are: (1) LACM 43717-1, 192 mm, which has five pores arising from ventral ramus and one from ascending ramus on right side, and five from ventral ramus and two from ascending ramus on left side; and (2) LACM 43717-1, 172 mm, which has suborbital pores two and four oddly doubled (pore at these positions are situated one atop the other) and no third pore, giving seven pores arising from ventral ramus and one from ascending ramus. Eight preoperculomanibular pores, four arising from dentary, one from anguloarticular and three from preopercle. Interorbital pores absent. Occipital (supratemporal) canal with single,

mesial pore in all. Body lateral line with medio-lateral branch originating on vertical about one eye diameter anterior to posterior margin of pectoral fin; mediolateral branch not visible in greatly faded juveniles in LACM 43717-1; ventral branch originating just posterior to fourth postorbital pore, gradually descending across abdomen to above anal fin base; both branches complete to tail tip.

Dorsal fin origin associated with vertebrae 4–5. Anal fin origin associated with ultimate precaudal vertebra (numbers 24–26), with 3–4 anal pterygiophores inserted anterior to haemal spine of first caudal vertebra. Last dorsal ray associated with second, fourth, or fifth preural vertebrae, last anal ray associated with second preural vertebra. Caudal fin with 1–2 epural, four upper hypural, and 4–5 lower hypural rays. Pelvic fins absent except in MNHNC 6653 and ZIN 48394 which have small, fleshy fins of three rays each.

Gill rakers on upper limb (epibranchial) of first arch moderately long, sharply pointed; ventral-most rakers on lower limb (ceratobranchial) of adult female and juveniles small, but sharply pointed, those of adult male blunt, with squared-off tips. Branchiostegal rays six. Pseudobranch filaments long, numbering 3–4.

Recently preserved specimens (collected 1978–1986) uniformly dark brown in alcohol, probably black in life. Eye blue. Peritoneum, lining of gill cavity and inner palate black. Outer palate and lips pale.

DISTRIBUTION.—Known from eight specimens taken off western South America from the upper slope to the edge of the Peru-Chile Trench, reliably known from depths of 760–1,830 m (Fig. 11). Capture depth of holotype unknown; from fisheries vessel.

ETYMOLOGY.—From the Greek μέσος (middle) and πόρος (hole, pore) in reference to the unique condition of the species' occipital canal with its single, mesial pore.

REMARKS.—This is the second species of *Pachycara* known in which pelvic fins are present or absent (the other is *P. sulaki*) and the fourth zoarcid reported with this condition (others are *Crossostomus chilensis* [see Gosztonyi 1977] and *Lycenchelys monstrosa* [see Anderson 1982b]). The two specimens with pelvic fins (ZIN 48394 and MNHNC 6653) also exhibit slightly elevated vertebral counts (111 and 113 vs. 103–106 for others), higher gill raker counts (16 and 18 vs.



FIGURE 14. *Pachycara pammelas* n. sp., CAS 62407, holotype, 336 mm SL, from off Punta Lobos, Chile.

13–15 for others), and higher pectoral ray counts (16 and 18 vs. 15–16 for others). It was tempting to consider the presence of two closely related species with mesial occipital pores in the sample of eight specimens. However, this unique condition, plus the identical lateral lines, squamation, and state of dentition, makes it apparent that the noted anatomical differences cannot be considered above the range of individual variation found in either other *Pachycara* species represented by larger sample sizes, or other zoarcids.

Pachycara pammelas n. sp.

(Figs. 11, 14)

HOLOTYPE.—CAS 62407 (female, 336 mm); off Punta Lobos, Chile (20°50'S, 70°27'W); Chilean fisheries vessel; trawl, 610 m; I. Kong Urbina, 21 Feb. 1981.

PARATYPES.—SIO 72-183 (2; 96–192 mm); off Arica, Chile (18°44.7'–40.2'S, 70°40.7'–35.1'W); South Tow Exped., 1,097–1,152 m; R. L. Wisner and party, 1152–1330 hr, 7 May 1972. LACM 43732-1 (2; 152–217 mm); off Coquimbo, Chile (30°06.0'S, 71°42.6'W); ANTON BRUUN sta. 708; free vehicle set line trap, 1,000 m; L. W. Knapp and party, 14 Aug. 1966. LACM 43726-1 (2; 226–231 mm); off Valpariso, Chile (33°39.0'S, 72°09.5'W); ANTON BRUUN sta. LWK 66-41; trawl, 1,170–1,480 m; L. W. Knapp and party, 10 Aug. 1966.

COUNTS AND MEASUREMENTS.—Vertebrae 23–26 + 81–88 = 105–114; D 99–109; A 83–92; C 10–11; P₁ 15–18; P₂ 3; vomerine teeth 3–9; palatine teeth 2–14; gill rakers 1–3 + 12–17 = 14–20; branchiostegal rays six; pseudobranch filaments 2–5. Following measurements in percent SL: head length 12.8–15.6; head width 5.7–9.0; pectoral fin length 7.1–9.2 predorsal length 15.0–18.4; preanal length 34.0–37.0; body height 6.3–10.5; gill slit length 4.0–6.4; caudal fin length 1.6–2.7. Following measurements in percent HL: head width 39.9–67.4; upper jaw length 34.1–52.7; pectoral fin length 50.8–64.2; snout length 15.6–22.2; eye diameter 19.5–30.4; gill slit length 25.7–50.2; interorbital width 6.7–8.9; interpupillary width 23.7–33.2; pelvic fin length 7.4–13.3. Pectoral base/length ratio 33.0–51.4.

DIAGNOSIS.—Pelvic fins present; origin of mediolateral lateral line immediately posterodorsal last postorbital pore; origin of ventral lateral line immediately posterior to last postorbital pore; vertebrae 23–26 + 81–88 = 105–114; no scales on nape.

DESCRIPTION.—Following description based on one adult female (holotype), two juvenile males, and four juvenile females. Head ovoid, snout bluntly rounded in females giving head more rounded appearance than males. Males (152 and 192 mm) with head elongate, dorsoventrally depressed, snout long, gently tapering. Scales extending anteriorly on body to nape where present in patch extending in front of dorsal fin origin in holotype (absent there in smaller paratypes); scales present on unpaired fins (except 96 mm juvenile), abdomen, pectoral axil and base (latter in holotype only). Eye ovoid, entering dorsal profile of head. Gill slit short, extending just to lower margin of pectoral base or slightly above. Lobe at dorsal margin of gill slit weak, gill slit not extending anteriorly in largest male; lobe rounded or squared-off. Pectoral fin origin well below body midline in larger specimens (closer to midline in smallest two), insertion on abdomen; posterior margin of fin evenly rounded, middle rays longest; ventralmost four or five rays thickened, tips very slightly exserted.

Mouth subterminal, oblique, snout more produced in males than females; upper jaw extending posteriorly to middle of eye in females, to just beyond its posterior margin in largest male. No epidermal prickles evident on snout or lips. Oral valve well developed, overhanging anterior margin of vomer in holotype, coalesced with sides of palate posterior to vomer in all. Jaw teeth small, blunt, conical; dentary with four irregular rows anteriorly in holotype, blending into single, posterior row consisting of 2–4 teeth; dentary teeth in two to four (largest two paratypes, LACM 43726-1) irregular anterior rows in others, blending into single, posterior row. Premaxilla with two anterior rows of teeth, blending into single,

posterior row except in smallest specimen (SIO 72-183, 96 mm) which has single row of nine teeth. Vomerine teeth in patch or arc (small specimens); palatine teeth blunt, not retrorse, in double row in holotype, single row in others.

Cephalic lateralis system with three postorbital pores arising from frontal (pore one), between pterotic and lateral extrascapular (pore three), and posterior to lateral extrascapular (pore four). Largest male (SIO 72-183, 192 mm) with pores one and four only. Two pairs of anterior supraorbital (nasal) pores, one set mesial to nasal tube, the other posteriorly. Seven suborbital pores, six arising from ventral ramus of bone chain and one from ascending ramus behind eye just ventral to first postorbital pore; eight suborbital pores on right side only in LACM 43732-1, 152 mm). Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular, and three from preopercle. Interorbital and occipital pores absent. Body lateral line difficult to detect in faded paratypes, clear in holotype; mediolateral branch originating about half an eye diameter or less posterodorsal to last (number four) postorbital pore; ventral branch originating immediately posterior to postorbital pore four; both branches complete to tail tip.

Dorsal fin origin associated with vertebra 4-5. Anal fin origin associated with ultimate or penultimate precaudal vertebrae (numbers 23-26), with 2-4 anal pterygiophores inserted anterior to haemal spine of first caudal vertebra. Last dorsal ray associated with fourth preural vertebra, last anal ray associated with second preural vertebra. Caudal fin with two epural, 4-5 upper hypural and four lower hypural rays.

Gill rakers on upper limb (epibranchial) of first arch simple, sharply pointed; rakers on lower limb (ceratobranchial) laterally compressed, with squared-off tips; six lower limb rakers in holotype with shallowly bicuspid tips. Branchiostegal rays six. Pseudobranch filaments 2-5, minute in smallest specimen.

Holotype uniformly black (paratypes faded), eye blue. Peritoneum, gill cavity and inner palate black. Outer palate and inner surface of lips pale. Adult female with ripe ova measuring 3.9-4.2 mm in diameter (not counted).

DISTRIBUTION.—Known from seven specimens captured along the edge of the Peru-Chile Trench off Chile at depths of 610-1,480 m (Fig. 11).

ETYMOLOGY.—From the Greek *παμ* (an intensifier meaning "all") and *μέλας* (black), a noun in apposition, alluding to the coloration of the species.

***Pachycara brachycephalum* (Pappenheim, 1912)**

Lycodes brachycephalus Pappenheim, 1912:179-180, pl. X, fig. 3.

Austrolycichthys brachycephalus (Pappenheim). Regan, 1913: 244-245, fig. 2; Waite, 1916:15, pl. I, text fig. 2, 2A; Norman, 1938:81, 83, 84.

Pachycara brachycephalus (Pappenheim). Anderson, 1988a: 74-77, figs. 16-19.

MATERIAL EXAMINED.—See Anderson (1988a:74-75).

LECTOTYPE (herein designated).—ZMB 18929 (male, 169 mm); Wilhelm Land, Antarctica; GAUSS winter station; fish traps, 385 m; Deutsche Südpolar Exped., 1902.

DIAGNOSIS.—Pelvic fins present; mediolateral lateral line originating just posterior to pectoral fin margin; ventral lateral line originating above dorsal edge of gill slit; scales absent on nape; vertebrae 23-27 + 71-86 = 95-113; D 88-107; A 72-90; P 16-18; dorsal fin origin associated with vertebrae 3-7; gill rakers 0-3 + 9-13 = 9-16; branchiostegal rays six; suborbital pores 5 + 1 (5 + 0 in one); postorbital pores 1-2; head length 14.0-19.9% SL; pectoral fin length 10.0-12.7% SL.

DISTRIBUTION.—Coastal Antarctica in inner basins and on outer slope at depths of 200-1,810 m.

DISCUSSION

So few specimens of *Pachycara* are known for most species that it is difficult to consider the evolutionary history of the genus. Phylogenetically, *Pachycara* seems to have arisen as a deep-slope sister taxon or precursor of *Lycodes*, differentiated by its reduced parasphenoid wing (apomorphy), retention of the oral valve and cephalic pores, and lack of developed mental crests (plesiomorphies; see Anderson 1984). *Thermarces* is derived with respect to *Pachycara* in four reductive characters: (1) absence of pelvic bones; (2) absence of scales; (3) absence of lateral lines; and (4) gelatinous flesh.

The present distributions of *Pachycara* species indicate two main historical biogeographic tracks: (1) North Atlantic-eastern Pacific; and (2) western South America-Antarctica (*P. brachycephala*).

lum). With only one specimen known, the origin and distribution of *P. shcherbachevi* (Indian Ocean) remains a mystery, but it appears closer to *P. bulbiceps* than the two West African species in its high vertebral count, small head, and retrograde dorsal fin origin. Recently, I reviewed the mid-Miocene tectonic history of the American tropics as it relates to the distribution of deep-sea bottom fishes (Anderson 1988a), and *Pachycara* in particular (Anderson and Peden 1988). I concluded that the closing of the Panamanian seaway to deep-demersal fishes about 7–10 million years ago did not sunder Atlantic and Pacific stocks of *P. bulbiceps* (if there were any), and that the present two populations possibly exchange genes through as yet unsampled South Pacific and South Atlantic populations (Anderson and Peden 1988). This type of distribution (Fig. 5) invites speculation on the origin and relationships of *P. sulaki*, presently known only from the western tropical Atlantic. This species expresses states of three characters that link it with southeastern Pacific forms (*P. mesoporum* and *P. rimae*) that may have phylogenetic utility: (1) possession of only five suborbital pores along the ventral ramus in some individuals; (2) dorsal fin origin retrograde, associated with vertebrae six to seven (*P. sulaki*) or eight (*P. rimae*); and (3) absence of pelvic fins in some individuals (*P. sulaki* and *P. mesoporum*). However, a phylogenetic analysis of *Pachycara* is precluded by uncertainty about the extent of distribution and the variability of many character states, particularly of the axial skeleton, dentition, cephalic pores, and the occasional lack of pelvic fins. This, in turn, produces a cautionary appraisal of the specific status of the present samples of *P. bulbiceps* (Pacific and Atlantic populations) and *P. mesoporum* (range of variation) that only future sampling may clarify.

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PROCEEDINGS
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A PHYLOGENETIC REVISION OF THE PHALLOSTETHID FISHES
(ATHERINOMORPHA, PHALLOSTETHIDAE)

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ABSTRACT: The Phallostethidae (including Neostethidae) comprises a group of small to minute atherinomorphic fishes distinguished from all other teleosts by the presence in males of a complex, bilaterally asymmetric, subcephalic copulatory organ, the priapium. I recognize 19 species in four genera: *Phallostethus* Regan, 1913, *Neostethus* Regan, 1916, *Gulaphallus* Herre, 1925, and *Phenacostethus* Myers, 1928. This includes one new species, *Neostethus robertsi*, from Luzon. Phallostethids are widely distributed throughout coastal brackish waters from Thailand, Singapore, Malaysia, and the Philippines, as well as inland freshwater streams of Luzon and Borneo.

The three objectives of this review are to: (1) describe the anatomy and variation of the priapium and propose synonymy and probable homology of its many and varied osteological and myological modifications; (2) present taxonomic synonymies and diagnoses of the 19 species in four genera; and (3) hypothesize phylogenetic relationships among the species by grouping into higher categories based primarily on the presence of shared derived characters of the priapium.

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INTRODUCTION

Regan (1913) named the first known phallostethid species *Phallostethus dunckeri* in honor of Georg Duncker (1904), who first reported this unusual group of fishes from Johore on the Malay Peninsula. During the following three decades, attention focused on description of new species and genera (e.g., Regan 1916; Herre 1925, 1926; Myers 1928; Villadolid and Manacop 1935; Manacop 1936), anatomy of the complex copulatory organ, the priapium (e.g., Bailey 1936; Aurich 1937; TeWinkel 1939; Woltereck 1942a, b), and consideration of the relationships of phallostethids to other fishes (e.g., Smith 1927; Myers 1935; Hubbs 1944).

Presence of a priapium led to speculation that phallostethids must be live bearers (e.g., Regan 1913). However, Smith (1927) observed female phallostethids in Thailand depositing eggs. Villadolid and Manacop (1935) confirmed that females of *Gulaphallus mirabilis* lay fertilized eggs following copulation. Structure of ovaries and testes, presence of sperm bundles (spermato-

zeugmata), and mode of internal fertilization are currently under investigation (Grier and Parenti, in prep.).

Early descriptions of phallostethids followed the convention of naming morphologically distinctive populations not just as new species but as new genera as well. In the last comprehensive review of phallostethids, Herre (1942) recognized 18 species classified in 10 genera, one of which had two subgenera (Table 1).

Interest in phallostethid systematics was renewed with description of a new species, *Phenacostethus posthon* Roberts, 1971a and a detailed osteological study of *Neostethus bicornis* Regan (formerly in *Ceratostethus*) (Roberts 1971b). Despite extensive work by Roberts, numerous questions remained concerning the relationships of phallostethids to other atherinomorphs, limits of, and relationships among, genera, and total number of recognizable species. It was with the goal of answering these questions that I began my studies of phallostethids.

A preliminary review resulted in detailed osteology of *Phallostethus dunckeri* and the proposal that phallostethids are the sister group of the Indo-Pacific atherinoid, *Dentatherina merceri* Patten and Ivantsoff, 1983 (Parenti 1984). I described a new species, *Phenacostethus trewavasae* Parenti, 1986a and brought the total number of then recognized species to 20. Homology of priapial structures, always a challenge to students of phallostethids, was considered by examining development of the pelvic fins of one species, *Gulaphallus falcifer* Manacop (formerly in *Manacopus*), in which there are bilaterally asymmetric adult females as well as males (Parenti 1986b). I (Parenti 1986c) reviewed the association between bones and teeth in teleost fishes because in some phallostethid species there is a perichondrally ossified lower jaw bone, the paradentary, that may possess teeth.

Much of the information compiled on phallostethid fishes has been inaccessible to, or ignored by, systematists because of the array of peculiar names applied to parts of the complex priapium and because of the small size of phallostethids. Further, no previous classifications summarize cladistic relationships adequately; rather, they emphasize gross phenetic differences among species.

Phallostethid fishes are distributed throughout coastal mainland and insular Southeast Asia from Thailand to the Philippines (Fig. 1), entirely west

of Wallace's Line, one of several hypothetical boundaries separating the Asian from the Australian biota (see Whitmore 1987). Cladistic relationships of phallostethids can be used to present a working hypothesis of the distributional history of one segment of the Indo-Australian biota (see methodology in Humphries and Parenti 1986). Results from this study will be combined with those of other analyses to prepare a historical biogeographic analysis of the Indo-Australian atherinomorph fishes (Parenti, in prep.).

This review has three objectives: (1) to describe the anatomy and variation of the priapium and propose synonymy and probable homology of its numerous osteological and myological modifications; (2) to present taxonomic synonymies and diagnoses of the herein recognized 19 species, with one described as new, classified in four genera; and (3) to hypothesize relationships among the species, grouping them into higher categories, primarily on synapomorphies of the priapium.

MATERIALS AND METHODS

I observed osteological characters on specimens counterstained with alcian blue and alizarin red S (Dingerkus and Uhler 1977) or stained solely with alizarin. I examined specimens with a Zeiss SV8 dissecting microscope and recorded data using a drawing tube and photomicrography attachments. Representatives of 18 of the 19 currently recognized phallostethid species were examined as part of my recent studies. No specimens of *Neostethus ctenophorus* (Aurich, 1937) were available; characters are from the original description.

Meristic data (except for scale counts) were tabulated from cleared and stained specimens. In recording meristic data (Table 2), the terminal half-centrum is counted as one vertebra, and all fin spines and rays are counted, including, for example, the last two anal rays which articulate with just one pterygiophore.

Institutional abbreviations follow the Standard Symbolic Codes for Institutional Research Collections in Herpetology and Ichthyology (Leviton et al. 1985). The following abbreviations are defined: Dist., district; Is., island; Prov., province; R., river; and SL, standard length. Catalog numbers for phallostethid material examined are given in the text.

TABLE 1. Comparison of Herre's (1942) classification of Phallostethids with that presented herein.

Herre (1942)	Present paper
<i>Phallostethus dunckeri</i>	<i>Phallostethus dunckeri</i>
<i>Phenacostethus smithi</i>	<i>Phenacostethus smithi</i>
	<i>Phenacostethus posthon</i>
	<i>Phenacostethus trewavasae</i>
<i>Mirophallus bikolanus</i>	<i>Gulaphallus bikolanus</i>
<i>Solenophallus thessa</i>	<i>Neostethus thessa</i>
<i>Gulaphallus eximius</i>	<i>Gulaphallus eximius</i>
<i>Gulaphallus mirabilis</i>	<i>Gulaphallus mirabilis</i>
<i>Ceratostethus bicornis</i>	<i>Neostethus bicornis</i>
<i>Manacopus falcifer</i>	<i>Gulaphallus falcifer</i>
<i>Neostethus</i> (<i>Neostethus</i>) <i>amaricola</i>	<i>Neostethus amaricola</i>
<i>Neostethus</i> (<i>Neostethus</i>) <i>lankesteri</i>	<i>Neostethus lankesteri</i>
<i>Neostethus</i> (<i>Neostethus</i>) <i>siamensis</i>	synonym of <i>Neostethus lankesteri</i>
<i>Neostethus</i> (<i>Neostethus</i>) <i>villadolidi</i>	<i>Neostethus villadolidi</i>
<i>Neostethus</i> (<i>Sandakanus</i>) <i>borneensis</i>	<i>Neostethus borneensis</i>
<i>Neostethus</i> (<i>Sandakanus</i>) <i>coronensis</i>	synonym of <i>Neostethus borneensis</i>
<i>Neostethus</i> (<i>Sandakanus</i>) <i>panayensis</i>	<i>Gulaphallus panayensis</i>
<i>Neostethus</i> (<i>Sandakanus</i>) <i>zamboangae</i>	<i>Neostethus zamboangae</i>
	<i>Neostethus robertsi</i>
<i>Ctenophallus ctenophorus</i>	<i>Neostethus ctenophorus</i>
<i>Plectrostethus palawanensis</i>	<i>Neostethus palawanensis</i>

The theory of phylogenetic reconstruction followed is that commonly referred to as phylogenetic systematics or cladistics, as outlined by Hennig (1966) and modified by numerous authors (see review by Wiley 1981). Genera and other higher taxa are defined as monophyletic by the sharing of homologous derived characters, termed synapomorphies. Species are defined as the smallest, recognizable, morphologically distinctive groups of males and females which may share homologous derived characters, termed autapomorphies.

For priapial characters, a state that is unique to a particular phallostethid species, or group of species, is treated as derived. This is a special case of the method of outgroup comparison (see Maddison et al. 1984) which is used to determine polarity of non-priapial characters. The following atherinomorph specimens were examined for outgroup comparison: *Bedotia* sp., aquarium material, CAS 44367 (1 of 3 counterstained); *Dentatherina merceri*, Moluccas, USNM 230374

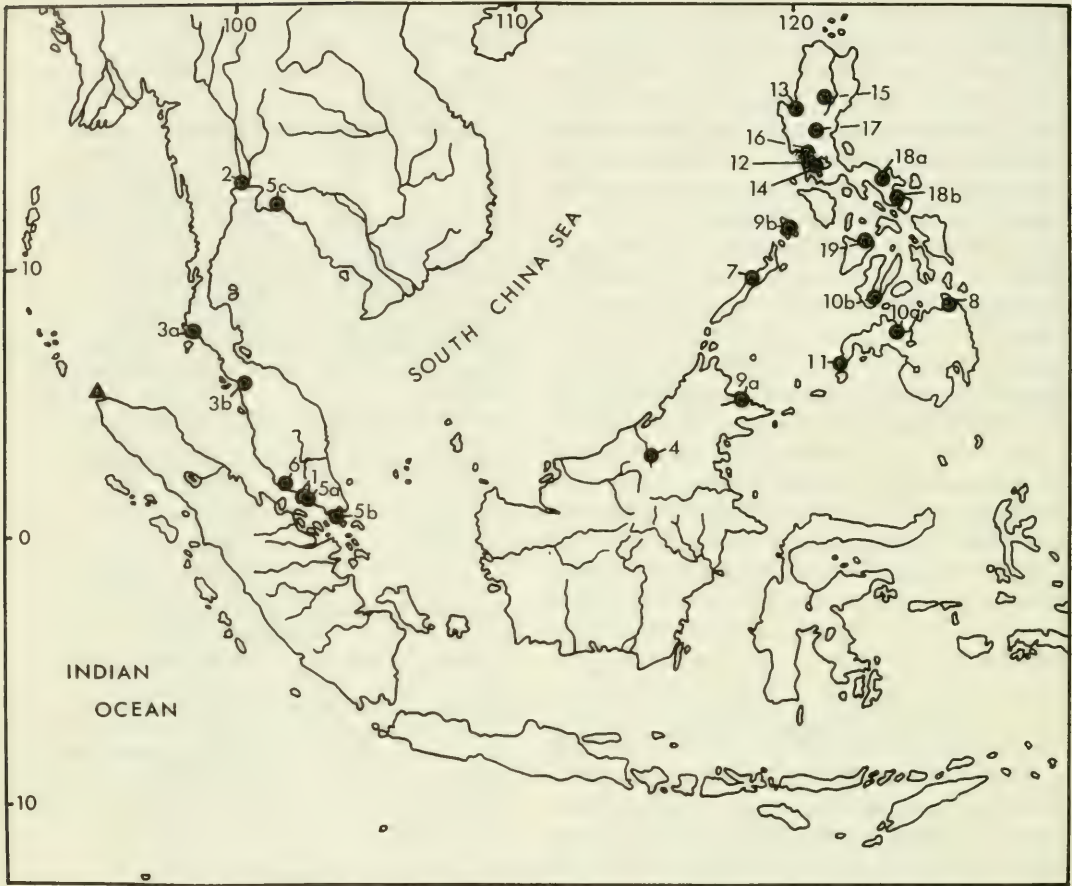


FIGURE 1. Distribution of phallostethids. Solid circles, type localities of the 19 currently recognized phallostethid species: 1. *Phallostethus dunckeri* Regan, Muar R.; 2. *Phenacostethus smithi* Myers, Bangkok; 3. *Phenacostethus posthon* Roberts, a. Khlong Kla Sohm, b. Khlong Langu; 4. *Phenacostethus trewasae* Parenti, Baram R.; 5. *Neostethus lankesteri* Regan, a. Muar R., b. Singapore, c. Chantabun R.; 6. *Neostethus bicornis* Regan, Kuala Langat; 7. *Neostethus palawanensis* (Myers), Ulugan Bay; 8. *Neostethus thessa* (Aurich), Lake Mainit; 9. *Neostethus borneensis* Herre, a. Sandakan Bay, b. Coron; 10. *Neostethus villadolidi* Herre, a. Misamis, b. Dumaguete; 11. *Neostethus zamboangae* Herre, Zamboanga; 12. *Neostethus amaricola* (Villadolid and Manacop), Pasay; 13. *Neostethus robertsi*, new species, Calasiao R.; 14. *Neostethus ctenophorus* (Aurich), Laguna de Bay; 15. *Gulaphallus eximius* Herre, Nueva Vizcaya; 16. *Gulaphallus mirabilis* Herre, Ibo R.; 17. *Gulaphallus falcifer* Manacop, Pampanga and Nueva Ecija; 18. *Gulaphallus bikolanus* (Herre), lakes Bato and Lanigay; and 19. *Gulaphallus panayensis* (Herre), Panay. Solid triangle, unsubstantiated report of unidentified phallostethid from off northwestern Sumatra by Aurich (1937).

(2 of 42 counterstained); *Hypoatherina ovalaia*, Vanuatu, Malekula Is., CAS 62564 (2 of 10 counterstained); *Melanotaenia affinis*, northern New Guinea, CAS 40573 (4 of 31 counterstained), and *Pseudomugil signifer*, New South Wales, Australia, CAS 62565 (6 of 62 counterstained).
The pattern of reduction or loss of a character, which is common in atherinomorphs, is useful as a source of information for phylogenetic reconstruction when correlated with other, more

complex characters (Parenti 1986b). Ontogenetic data are used to infer homology among character states (Patterson 1982) and as an additional source of information for character polarity (Nelson 1978). Ontogenetic transformation and pattern of reduction or loss are the most reliable sources of information on polarity of states of the priapium. Outgroup comparison is limited because a priapium is not found, even in a simplified condition, outside the Phallostethidae.

TABLE 2. Meristic characters of phallostethids. D1 = first dorsal rays, D2 = second dorsal rays, A = anal rays, P1 = pectoral rays, BR = branchiostegal rays, V = vertebrae, SLS = scales in lateral series.

Species	D1	D2	A	P1	BR	V	SLS
<i>N. lankesteri</i>	2	6-7	16-17	11-12	5	34-35	31-32
<i>N. bicornis</i>	1	5-6	15-16	10-11	5-6	36-37	31-34
<i>N. palawanensis</i>	1	5-6	15-16	11	5	34-35	30-32
<i>N. thessa</i>	0	8-10	17-22	12-13	5	36-37	32-34
<i>N. borneensis</i>	1-2	5-6	13-16	10-12	5	31-32	25-27
<i>N. robertsi</i>	2	6	17-18	10-11	5	36	30
<i>N. villadolidi</i>	2	5-6	14-16	9	5-6	35-36	30-32
<i>N. zamboangae</i>	2	5-6	15-17	9	5-6	35-36	29-32
<i>N. amaricola</i>	1-2	5-6	16	10-11	5-6	35-36	32
<i>N. ctenophorus</i> ^a	2	5-7	14-17	10-11	—	—	31-33
<i>G. eximius</i>	1-2	7-8	15-18	11	5	36-37	52-58
<i>G. mirabilis</i>	1-2	7	17-18	10-12	5	36-37	36-38
<i>G. falcifer</i>	1-2	8	17	10	5	35	32
<i>G. bikolanus</i>	0	6	14-17	11-13	5	35-36	32
<i>G. panayensis</i>	1-2	6-7	13-15	11	5	31-33	28-30
<i>P. dunckeri</i>	0	8-10	26-28	9-10	4	40	^b
<i>P. trewavasae</i>	1	6	14-15	9-10	5	34	^b
<i>P. posthon</i>	1	5-6	14-15	9-10	4	34-35	^b
<i>P. smithi</i>	1	6-7	14-15	9-10	4-5	33-35	^b

^a From Aurich (1937).
^b Because Phallostethini scales are small and deciduous, it is difficult to record an accurate count.

RELATIONSHIPS OF PHALLOSTETHIDS TO
OTHER ATHERINOMORPHS

None has questioned monophyly of the phallostethids, i.e., all phallostethid males have a priapium, and none has argued that the priapium is not a uniquely evolved structure. I present no argument here to contradict phallostethid monophyly. However, I acknowledge that information from some future study could lead us to conclude that not all priapia are homologous.

Perhaps the only currently controversial aspect of phallostethid systematics is their relationship to other acanthopterygian fishes. The following four issues, with references for arguments pro and con, summarize the debate:

1. Atherinomorphs are monophyletic, although their relationship to other acanthomorph teleosts remains obscure (Rosen 1964; Rosen and Parenti 1981; Collette et al. 1984; Parenti 1981, 1984; Grier and Collette 1987).

Since Rosen (1964) formally recognized the series Atherinomorpha, which comprises the atherinoids, cyprinodontiforms, and beloni-forms, the group has been accepted by ichthyologists, although with some reservation (e.g., Roberts 1971b). However, it is generally agreed that systematic differences between the Ather-

inidae and Cyprinodontidae are not as great as had been thought by Hubbs (1944). Traditional groups such as the Percosoces—which contains the mullets (Mugiloidea), polynemids (Polyne-moidea), and phallostethids (Phallostethoidea), according to the classification of Myers (1937)—are no longer recognized. However, possible atherinomorph relatives may be among constituents of these taxa, such as the mugilids. Confirmation of the sister group of the Atherinomorpha, as well as other acanthomorph taxa, is the subject of ongoing studies by numerous systematic ichthyologists, including myself, and will not be discussed further here.

2. Phallostethids are atherinomorphs (Rosen and Parenti 1981; Parenti 1984; White et al. 1984; Ivantsoff et al. 1987), or may be related to polynemids (Bailey 1936) or to gobioids (Springer 1983).

Determining whether phallostethids are atherinomorphs requires a well-corroborated definition of the series Atherinomorpha; phallostethids either fit the definition or they do not. Rosen and Parenti (1981) listed defining characters of the Atherinomorpha, which includes a derived ethmoid region and hyobranchial apparatus. Recent workers have corroborated the

proposal that the Atherinomorpha is monophyletic (e.g., Grier and Collette 1987), and that phallostethids are atherinomorphs (Parenti 1984; Ivantsoff et al. 1987).

Bailey (1936) hypothesized a close relationship between phallostethids and polynemids based on the shared close association of the pelvic and pectoral girdles. Springer (1983) cited shared reductions between phallostethids and gobioids to suggest, in a footnote, their possible close relationship. To endorse the hypothesis that phallostethids are atherinomorphs requires that the characters shared by phallostethids and polynemids or gobioids be treated as convergent. However, Springer's (1983) proposal expands the list of possible atherinomorph close relatives to polynemids, mullets, and gobioids.

3. Atherinoids, including the silversides (or hardyheads), rainbowfishes, and phallostethids, are not monophyletic (Rosen and Parenti 1981; Parenti 1984; Ivantsoff et al. 1987) or atherinoids are monophyletic (White et al. 1984).

Rosen and Parenti (1981) and Parenti (1984) proposed that atherinoids do not constitute a monophyletic group because they exhibit transformation series for certain characters, such as transformation of the first dorsal fin from pleiomorphic atherinoids (e.g., *Bedotia* and *Melanotaenia*) in which it is well developed, to phallostethids in which it is reduced or absent. This view was supported by Ivantsoff et al. (1987). White et al. (1984) proposed two developmental characters to support their view that atherinoids are monophyletic. This issue will be clarified when there is a well-corroborated proposal of relationships among the major groups of atherinomorph fishes, a study under progress.

4. Phallostethids are the sister group of *Dentatherina* Patten and Ivantsoff, 1983 (Parenti 1984), or the close relationship of phallostethids to *Dentatherina* is not supported (Ivantsoff et al. 1987).

Parenti (1984) proposed a close relationship between *Dentatherina merceri* and phallostethids based on, among other characters, presence of a paradentary bone. At issue is whether the paradentary elements—ossifications of the labial ligament—are homologous in phallostethids and *Dentatherina*. The phallostethid paradentary bone is composed of acellular bone surrounding hyaline cartilage (Parenti 1986c; Ivantsoff et al. 1987). The *Dentatherina* paradentary bone is

composed of hyaline cartilage with a calcified core (Ivantsoff et al. 1987).

Ivantsoff et al. (1987) cited the histological differences between the phallostethid and *Dentatherina* paradentary elements to conclude that the bones are not homologs and, therefore, cannot be used to propose a close relationship between two taxa. They also rejected homology based on the conclusion that calcification or ossification in a labial ligament could result as a response to stress. I concur that if the bones are not homologous they cannot be used to propose a close relationship between two taxa. However, I reject the functional argument against homology. The labial ligament could become calcified or ossified in any taxon in which it occurs; within atherinomorphs, it is reported ossified only in phallostethids and *Dentatherina*. In my opinion, additional characters are needed to accept or refute the proposal of a phallostethid-*Dentatherina* sister group.

Phallostethids need no additional support to be accepted as a monophyletic group; a seemingly endless number of derived characters could be listed to define them (see Synonymy and Homology of Priapial Structures). Further research should focus on the question: to which group of Old World atherinoids are phallostethids most closely related? Hubbs (1944:70) summarized the importance of this type of question in systematics: "Whether or not a suborder or an order be recognized for the Phallostethidae, on the basis of the bizarre copulatory organ (the priapium) and of other structures, is, like most questions of ranking, of no great inherent significance. Whether the relationship of the family is with Cyprinodontidae or with the Atherinidae, or with neither, is a problem of greater meaning."

SYNONYMY AND HOMOLOGY OF PRIAPIAL STRUCTURES

Since Regan (1913) first described the complex anatomy of the phallostethid priapium, students of this unusual group of fishes have struggled to attain a stable, appropriate set of terms for the numerous priapial structures (Regan 1916; Bailey 1936; Aurich 1937). Nearly every paper discussing priapial anatomy contains errors of identification or proposed homology. A common mistake is to refer to the same structure by more than one name in a single paper.

Proliferation of names for priapial structures was encouraged by Regan (1916), who believed that the priapium was a new morphological structure with no known homolog among teleost fishes. For example, Regan gave the adjectival name "anterior infrasulcar" to a bone which I consider the homolog of one of the pelvic bones.

No doubt, a stable nomenclature has not been attained because homology of the priapial structures has not been well understood, and because structure of the priapium may vary greatly from one phallostethid genus to another. Bailey (1936) concluded that priapia of *Phenacostethus smithi* and *Gulaphallus mirabilis*, and hence of all phallostethids, correspond bone-for-bone. Furthermore, he believed that these structures could be identified in polynemids, close relatives of phallostethids according to Bailey. However, he did not examine a species of *Neostethus*, which has bony elements not found in either *Phenacostethus* or *Gulaphallus*. Also, a close relationship between polynemids and phallostethids has not been supported (see Relationships of Phallostethids to other Atherinomorphs).

The priapium may be thought of as having three structural and functional components: suspensory, holding or clasping, and papillary (Bailey 1936). The suspensory component consists of expanded anterior pleural ribs, including anteriorly expanded cleithra in *Neostethus* and *Gulaphallus*, as well as modified pelvic bones. The holding or clasping component consists of the externalized ctenactinia and/or toxactinium, the movement of which is controlled mainly by a set of longitudinal muscles. The papillary component consists of the seminal and infrasulcar papillae and papillary bones used in the transfer of sperm bundles from males to females.

To describe the diverse and detailed priapia of phallostethids, I have compiled a synonymy of priapial structures (Table 3 and below). In addition, I propose, where possible, the homolog of each element as found in relatively unmodified atherinoid fishes. Listed is the name of a structure, first and subsequent citations, including misidentifications, in major papers on phallostethids, brief description, probable homolog, known synonyms, and citations.

antepleural cartilage or bone (Figs. 2, 3)—Regan (1916:7), Roberts (1971b:408), Parenti (1986a:228). A large block of cartilage, sometimes par-

tially or fully ossified, that lies anterior to the distal tips of the first pleural ribs in males.

apocrocal side or aspect—Regan (1913:552, 1916:5), Herre (1942:138), Parenti (1986a:225). That side of the male's body without the anal opening. Male phallostethids are bilaterally asymmetric such that the anus and seminal papilla are offset to opposite sides of the body (see Parenti 1986a).

axial bone—Regan (1916:7), Bailey (1936:464), TeWinkel (1939:61), Villadolid and Manacop (1935:215). An elongate bone with rodlike spine and broad, dorsal crest. The apocrocal and procal axial bones are homologous with the pelvic bones (Regan 1913, 1916; Bailey 1936).

apocrocal axial bone (Figs. 2–5)—Roberts (1971b:408–409). The axial bone on the apocrocal side of the body. Synonyms: anterior infrasulcar bone (Regan 1916:8, Bailey 1936:466), desmactinium (Aurich 1937:267), ctenactinium (misidentification, Herre 1925:508, 1926:539; Myers 1937:142), second ctenactinium (misidentification, Bailey 1936:463), short ctenactinium (misidentification, Villadolid and Manacop 1935:195).

procal axial bone (Figs. 3–5)—Roberts (1971b:408–409). The axial bone on the procal side of the body, with which the toxactinium and ctenactinia articulate. Synonym: axial bone (Regan 1916:7; Myers 1935:5; Bailey 1936:464; Parenti 1986a:228, 1986b:308).

ctenactinium—Regan (1913:552, 1916:5), Myers (1928:1, 1935:5), Bailey (1936:465–466), Manacop (1936:376), Aurich (1937:264), TeWinkel (1939:62), Herre (1939:140, 1942:138), Woltereck (1942b:339), Roberts (1971a:6, 1971b:393), Parenti (1984:6, 1986b:309). One of two curved, rodlike priapial bones that articulate with the posterior end of the procal axial bone. Homologous with a pelvic fin ray (Bailey 1936).

first ctenactinium (Figs. 3–5)—The prominent, elongate externalized priapial bone in *Neostethus* and *Gulaphallus*. Usually called the ctenactinium, referred to herein as the first ctenactinium to distinguish it unambiguously from the second ctenactinium. Synonym: toxactinium (misiden-

TABLE 3. Summary of names of priapial structures and synonyms. See text for definitions and references.

Priapial structure	Synonyms
antepleural cartilage or bone	
aproctal side or aspect	
axial bone	
aproctal axial bone	anterior infrasulcar bone, desmactinium, ctenactinium, second ctenactinium, short ctenactinium
proctal axial bone	axial bone
ctenactinium	
first ctenactinium	toxactinium
second ctenactinium	Priapklauē, "pulvinular spine," anterior infrasulcar bone
efferent groove	
epididymis	
fringe	terminal coil of vas deferens comblike projections, comblike cilia, cilia, comb
glandular groove	
infrasulcar bones	
anterior infrasulcar bone	aproctal axial bone
posterior infrasulcar bone	
infrasulcar prominence or papilla	
keel	embryonic fin-fold, fringe
longitudinal muscles	
ctenactinial muscle	
outer muscle of aproctal side	
inner muscle of proctal side	
muscle of proctal side	
papillary bones	penial bones
penial bone	
basipenial bone	
papillary bone	
prepapillary bone	
cristate bone	
pleuro-priapial muscle	
priapial process of cleithra	
priapial ribs	first pleural ribs
aproctal priapial rib	first pleural rib on aproctal side
proctal priapial rib	first pleural rib on proctal side
priapium	
proctal side or aspect	
pulvinular appendage	
pulvinular spine	
pulvinular bones	
inner pulvinular bone	
outer pulvinular bone	toxactinium

TABLE 3. Continued.

Priapial structure	Synonyms
pulvinulus	shieldlike pad, pulvinular pad
seminal papilla	genital papilla, penis
toxactinium	outer pulvinular bone, pulvinular bone, toxactinial bone, inner pulvinular bone, modified pulvinulus
uncus	

tification, Herre 1925:508, 1926:539; Villadolid and Manacop 1935:200).
second ctenactinium (Figs. 2, 4, 5, 9)—The shorter of the two externalized priapial bones that may have serrations, as in *Phallostethus*, and *N. zamboangae*. Synonym: Priapklauē (Aurich 1937:267), "pulvinular spine" or tip of anterior infrasulcar bone (misidentification, Herre 1942:138).

efferent groove—Regan (1916:5). A groove on the aproctal side of the body, posterior to the glandular groove and separated from it by the seminal papilla and infrasulcar prominence or papilla.

epididymis (Fig. 5)—Regan (1913:555), Roberts (1971a:6), Parenti (1986a:231). The coiled vas or ductus deferens enclosed in a membranous sac at posterior extent of the priapium. Synonym: terminal coil of vas deferens (Regan 1916:4).

fringe (Figs. 3, 13)—Regan (1916:5), Roberts (1971b:408). Posterior ends of pelvic fin rays that extend beyond the posteroventral outline of the epididymis. Synonyms: comblike projections (Myers 1928:8; Villadolid and Manacop 1935:197), comblike cilia (Herre 1939:140), cilia (Herre 1942:138), comb (Roberts 1971b:408).

glandular groove—Regan (1916:5). A groove on the aproctal side of the body at the boundary between the priapium proper and the body wall.

infrasulcar bones—Regan (1916:8). Two bones, referred to by Regan (1916) as the anterior and posterior infrasulcar, that, in part, support the infrasulcar and seminal papillae.

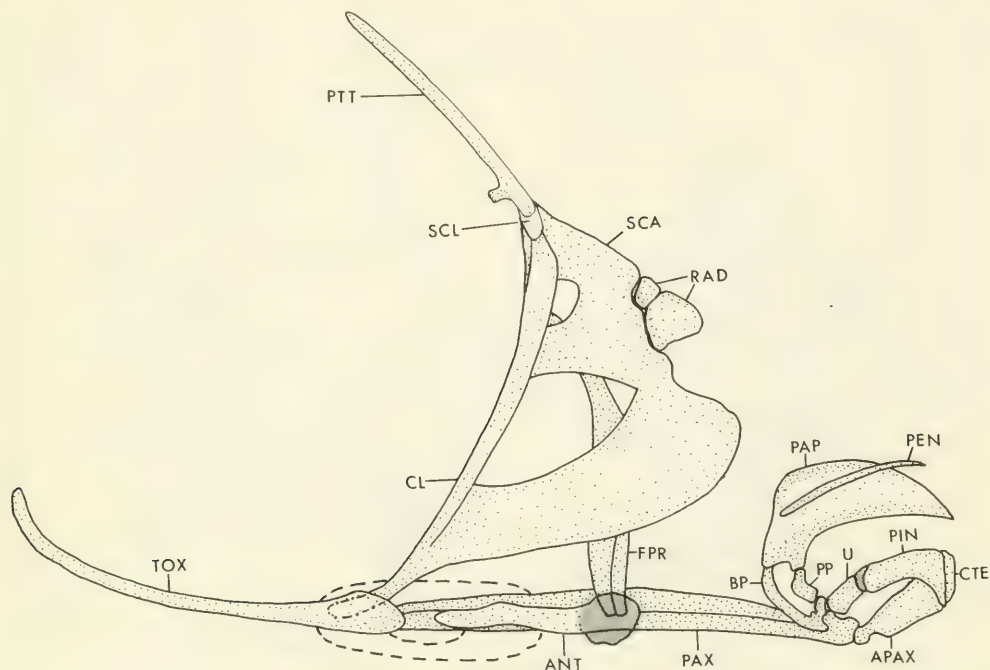


FIGURE 2. Diagrammatic representation of modified pelvic and pectoral fins in the priapium of a dextral male, *Phenacostethus smithi* (CAS-SU 35957 and modified in part from Bailey 1936), slightly exploded view from proctal side. Anterior to left. Dashed line, outline of pulvinulus; dotted and dashed line, anterior extent of cleithrum. Dense stippling, cartilage; light stippling, bone. Abbreviations: ant, antepleural bone and cartilage; apax, aproctal axial bone; bp, basipenial bone; cl, cleithrum; cte, second ctenactinium; fpr, first pleural ribs; pap, papillary bone; pax, proctal axial bone; pen, penial bone; pin, posterior infrasulcar bone; pp, prepapillary bone; ptt, posttemporal bone; rad, radials; sca, scapulocoracoid; scl, supracleithrum; u, uncus.

anterior infrasulcar bone—Regan (1916:8).
See aproctal axial bone.

posterior infrasulcar bone (Fig. 2)—Regan (1916:8), Bailey (1936:467). A rod-shaped bone at the base of the aproctal axial bone with a laminar projection that lies ventral to the aproctal axial bone, reaching the base of the infrasulcar papilla or prominence.

infrasulcar prominence or papilla—Regan (1916: 5, 8), Herre (1939:141). A papilliform projection anterior to the seminal papilla, supported internally by a posterior projection of the aproctal axial bone.

keel—Regan (1913:550), Myers (1935:5), Roberts (1971b:410). A median, abdominal, slightly frayed, fleshy ridge between the urogenital opening and anterior rays of the anal fin. Homologous with embryonic fin-fold (Roberts 1971b). Synonym: fringe (alternate

term not homologous with fringe as defined above, Regan 1916:2; Myers 1928:5).

longitudinal muscles (Fig. 6)—Regan (1916:13, fig. 10; 1916:14). Four fusiform muscles—ctenactinial muscle, outer muscle of the aproctal side, inner muscle of the aproctal side, and muscle of the proctal side—that originate on the axial bones and control copulatory movements of the priapium. Precise homology with pelvic fin muscles (Winterbottom 1974) is unclear.

ctenactinial muscle (Fig. 6)—Regan (1916: 14). Largest of the longitudinal priapial muscles, with an origin at the anterior end of the dorsal crest of the aproctal axial bone and insertion at the proximal end of the ctenactinium.

outer muscle of the aproctal side (Fig. 6)—Regan (1916:14). An elongate muscle that originates on the concave, aproctal side of the main crest of the proctal axial bone

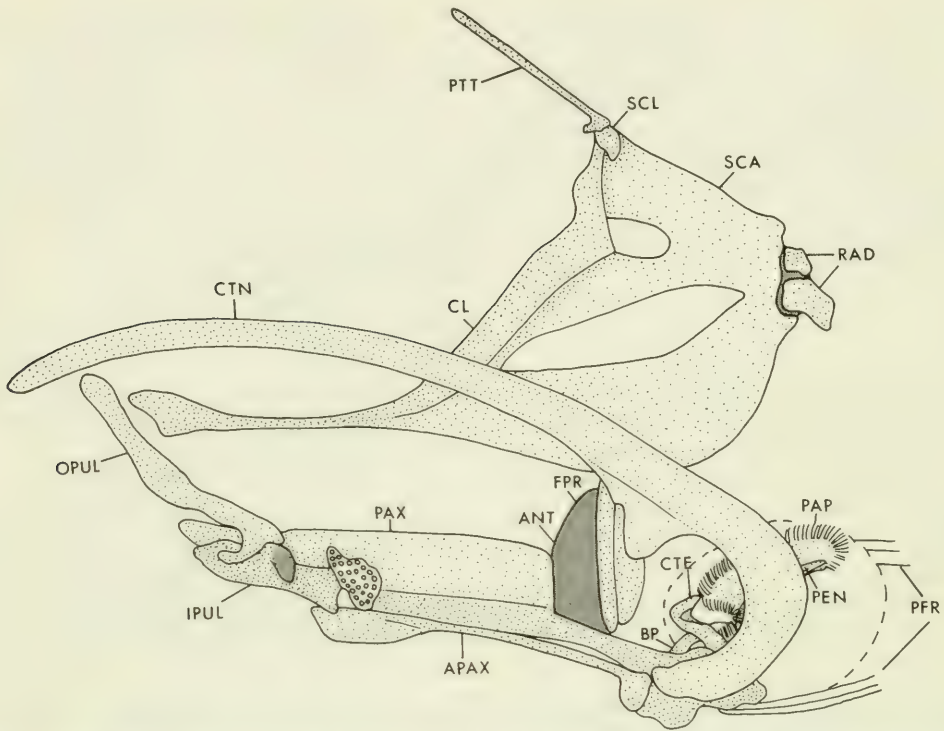


FIGURE 3. Diagrammatic representation of modified pelvic and pectoral fins in priapium of a sinistral male, *Neostethus lankesteri* (CAS-SU 67162). Anterior to left. Dense stippling, cartilage; light stippling, bone. Open circles, fibrous connective tissue of pulvinular appendage. Dotted line approximates outline of epididymis. Abbreviations: apax, aproctal axial bone; bp, basipenial bone; cl, cleithrum; cte, second ctenactinium; ctan, first ctenactinium; fpr, first pleural ribs; ipul, inner pulvinular bone; opul, outer pulvinular bone; pap, papillary bone; pax, proctal axial bone; pen, penial bone; pfr, pelvic fin rays; ptt, posttemporal bone; rad, radials; sca, scapulocoracoid; scl, supracleithrum.

and inserts on the base of the papillary bone.

inner muscle of the proctal side (Fig. 6)—Regan (1916:14). An elongate muscle that originates at the junction of the main crest of the proctal axial bone, internal to the outer muscle of the aproctal side, and inserts on a process of the proximal end of the toxactinium or outer pulvinular bone. muscle of the proctal side (Fig. 6)—Regan (1916:14). A muscle that originates at the extreme anterior end of the axial bone, with a few fibers at the posterior base of the toxactinium, posteriorly produced into a long tendon that inserts on the base of the papillary bone.

papillary bones (Figs. 2–4)—Regan (1916:8), Parenti (1984:6). Five small posterior priapial bones. Synonym: penial bones (Bailey 1936:467).

penial bone (Figs. 2–4)—Bailey (1936:467).

A thin, laminar bone that projects into the seminal papilla.

basipenial bone (Figs. 2–4)—Bailey (1936:465, 468). A rodlike bone that articulates with the base of the penial bone and posterior border of the cristate bone.

papillary bone (Figs. 2–4)—Regan (1916:8), Bailey (1936:468), Herre (1939:143). A slender, curved bone that supports the seminal papilla.

prepapillary bone (Fig. 2)—Bailey (1936:468). A slender, rodlike bone that articulates proximally with the basipenial bone and distally with the papillary bone.

cristate bone—Bailey (1936:469). A flattened, platelike bone that lies between the papillary bone and the aproctal axial bone and projects into the base of the seminal papilla.

pleuro-priapial muscle (Fig. 6)—Regan (1916:12).

A thin muscle that originates on the enlarged

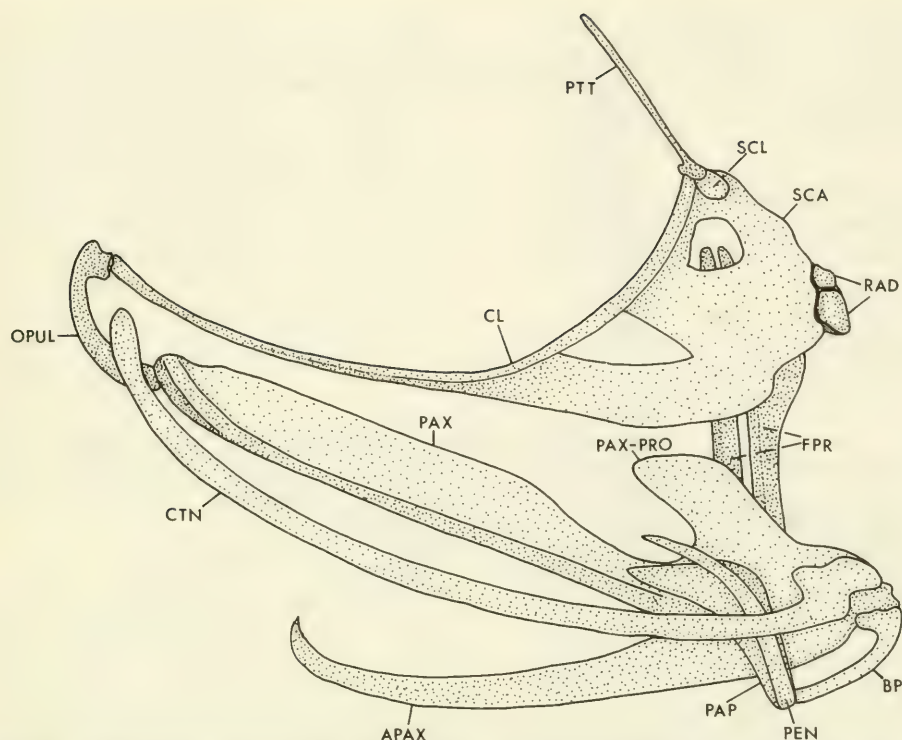


FIGURE 4. Diagrammatic representation of modified pelvic and pectoral fins in priapium of a sinistral male, *Gulaphallus mirabilis* (CAS-SU 38904 and modified in part from Bailey 1936). Anterior to left. Dense stippling, cartilage; light stippling, bone. Abbreviations: apax, aproctal axial bone; bp, basipenial bone; cl, cleithrum; ctn, first ctenactinium; fpr, first pleural ribs; opul, outer pulvinular bone; pap, papillary bone; pax, proctal axial bone; pax-pro, process of the proctal axial bone; pen, penial bone; ptt, posttemporal bone; rad, radials; sca, scapulocoracoid; scl, supracleithrum.

transverse process of the third or fourth vertebra on the proctal side and inserts on the proctal axial bone at the point of articulation of the first ctenactinium.

priapial process of cleithra (Figs. 3, 4)—Regan (1913:553–554). Anterior prolongation of the cleithra in *Neostethus* and *Gulaphallus*.

priapial ribs (Figs. 2–4)—Bailey (1936:463–464). The first pleural ribs on the third or fourth vertebra, modified to support the priapium.

aproctal priapial rib—Bailey (1936:464). The first pleural rib on the aproctal side of the body.

proctal priapial rib—Bailey (1936:463). The first pleural rib on the proctal side of the body.

priapium (Figs. 2–5, 9)—Regan (1913:551, 1916: 4), Myers (1928:1), Bailey (1936:453), Aurich (1937:263), TeWinkel (1939:59), Woltereck (1942a:254, 1942b:338). The subcephalic cop-

ulatory organ of phallostethid fishes comprising a bony portion used to hold the female during mating, a fleshy copulatory organ or seminal papilla through which sperm bundles

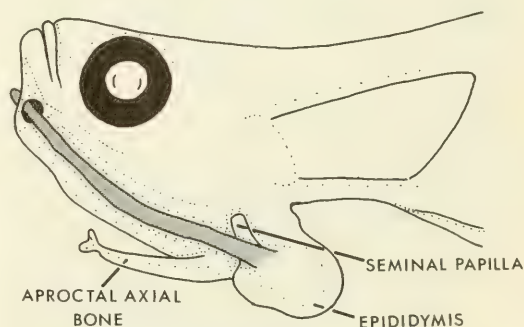


FIGURE 5. Diagrammatic representation of head and anterior portion of body, *Gulaphallus mirabilis*, sinistral male (CAS 50720). Anterior to left. Dense stippling, first ctenactinium.

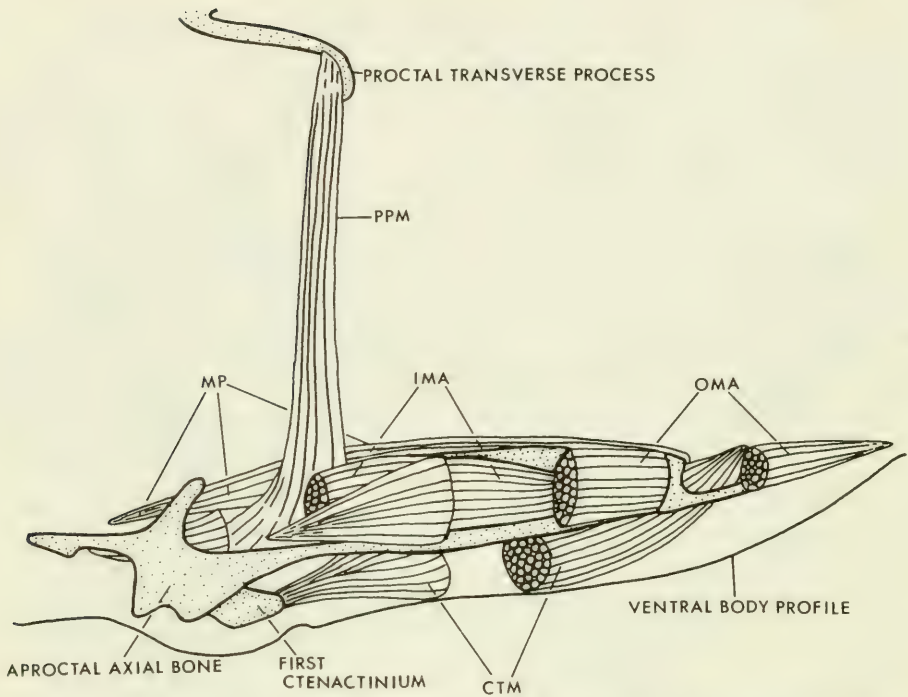


FIGURE 6. Schematic diagram of priapial muscles (modified from Regan 1916:fig. 10). Anterior to right. Stippling, bone. Abbreviations: ppm, pleuro-priapial muscle; ctm, ctenactinial muscle; mp, muscle of proctal side; ima, inner muscle of aproctal side; oma, outer muscle of aproctal side.

pass, and expanded cleithra and pleural ribs for suspension.

proctal side or aspect—Regan (1913:551, 1916:5), Herre (1942:138), Parenti (1986a:233). That side of the body with the anal opening.

pulvinular appendage (Fig. 3)—Regan (1916:5, 8), Herre (1942:137). A subconical, compressed mass of fibrous tissue that lies just posterior to the pulvinulus and is supported by the inner pulvinular bone in *Neostethus*.

pulvinular spine (Fig. 3)—Regan (1916:5, 9). A pointed, curved process of the toxactinium (=outer pulvinular bone).

pulvinular bones (Figs. 2–4)—Regan (1916:8–9). Two bones, termed an inner and an outer pulvinular, that articulate with the anterior end of the proctal axial bone.

inner pulvinular bone (Fig. 3)—Regan (1916:8–9). A longitudinal, chondral bone that lies anteroventral to the proctal axial bone.

outer pulvinular bone (Figs. 2–4)—Regan (1916:9). See toxactinium.

pulvinulus (Figs. 2, 9)—Regan (1916:5, 8), Myers (1928:6, 1935:5), Villadolid and Manacop (1935:194), Manacop (1936:376), Aurich (1937:264), Herre (1939:140), TeWinkel (1939:62), Roberts (1971a:7). Fibrous tissue surrounding the inner pulvinular bone and/or toxactinium (=outer pulvinular bone) covering point of articulation of the toxactinium, cleithra, and proctal axial bone. Synonyms: shieldlike pad (Bailey 1936:454); pulvinular pad (Parenti 1986a:230).

seminal papilla (Fig. 5)—Regan (1916:5), Herre (1939:143). A papilliform projection lying posterior to the infrascular prominence, supported internally by the posterior infrascular bone. Synonyms: genital papilla (TeWinkel 1939:62), penis (Roberts 1971a:1; Parenti 1986a:228).

toxactinium (Figs. 2–4)—Regan (1913:551), Myers (1928:1), Bailey (1936:462), Woltereck (1942b:339), Herre (1939:140, 1942:138), Roberts (1971a:6), Parenti (1986a:228). A rodlike, longitudinal bone, the posterior end

of which movably articulates with the symphysis of the cleithra and anterior end of the proctal axial bone. In *Phallostethus* and *Phenacostethus*, the anterior, distal end curves below the head towards the aproctal side of the body. Called the outer pulvinular bone in all other phallostethids, in which the anterior end articulates with the anterior end of the urohyal and the first basibranchial bone. Synonyms: outer pulvinular bone (Regan 1916:9), pulvinular bone (Bailey 1936:463), toxactinial bone (Bailey 1936:471), inner pulvinular bone (misidentification, Roberts 1971b:393), modified pulvinulus (Parenti 1984:6).

uncus (Fig. 2)—Bailey (1936:465, 467). A U-shaped chondral bone that articulates with the proctal axial bone posteriorly.

PHYLOGENETIC ANALYSIS

External morphology and osteology of the priapium has been reported in detail for a variety of phallostethid species (e.g., Regan 1913, 1916; Bailey 1936; Aurich 1937; TeWinkel 1939; Roberts 1971a, b; and Parenti 1984, 1986a). However, this represents the first attempt to summarize derived priapial and other characters within all phallostethid fishes, and to use corroborated hypotheses of synapomorphies to diagnose monophyletic genera and groups of genera.

Aurich (1937:285) perhaps came the closest to the goal of diagnosing groups of genera by tabulating identifying characters of his three subfamilies (but called "Familien")—Phallostethinae, Neostethinae, and Gulaphallinae—recognized herein at the tribal level with modified definition and composition. Aurich did not treat relationships among his three subfamilies, nor did he indicate which of the listed characters are what we would today recognize as derived or apomorphic.

Herre (1942) provided a synopsis of all genera and species, except *Phallostethus* and *Phenacostethus*, both then monotypic. I find many of Herre's (1942) characters, especially of scales, unworkable in a phylogenetic analysis. For example, number of scales on the opercle was used to divide *Neostethus* species into subgenera *Neostethus* and *Sandakanus*. Herre (1942:153) described several new species, including *N. panayensis*, treated as closely related to *N. zamboangae* Herre, 1942 and *N. coronensis* Herre,

1942, with which it shares two scales on the opercle. However, in priapial morphology, *N. panayensis* is a member of the monophyletic *Gulaphallus* as defined below, and not closely related to *N. zamboangae* or *N. coronensis* (= *borneensis*, herein).

Roberts (1971b:396) published a diagram in which relationships among the then recognized nine genera were summarized. It was not Roberts's purpose to provide a phylogenetic revision of all phallostethids; however, like Herre, Roberts depicted the monotypic *Manacopus* as closely related to *Neostethus*; *Manacopus* is considered a synonym of *Gulaphallus* herein.

Monophyly of Phallostethidae

As stated in the section Relationships of Phallostethids to other Atherinomorphs, phallostethid fishes have been considered monophyletic since Regan's (1916) review of the then three known species: by definition, all phallostethid males have a priapium, a complex structure not found in any other group of fishes. It is perhaps impossible to tabulate all the characters in phallostethids that have undergone transformation from the state in plesiomorphic atherinoids. Over 30 modifications of pelvic and pectoral bones, muscles, and cartilage can be identified (see Synonymy and Homology of Priapial Structures).

Further, presence of a keel, homologous with the ventral embryonic fin-fold as reported by Takita and Nakamura (1986) in larval *Hypoatherina bleekeri*, and other paedomorphic characters in all phallostethids suggest that evolution of a priapium is correlated with maturation at a relatively small size. Congruence (Mickevich 1978) exists between patterns of loss and reduction associated with small size and development of some complex priapial characters, especially within phallostethins.

Relationships of Subfamilies and Tribes

The following classification summarizes phylogenetic relationships among the tribes and subfamilies of phallostethids I recognize:

- Family Phallostethidae
 - Subfamily Phallostethinae
 - Tribe Phallostethini
 - Tribe Neostethini
 - Subfamily Gulaphallinae
 - Tribe Gulaphallini

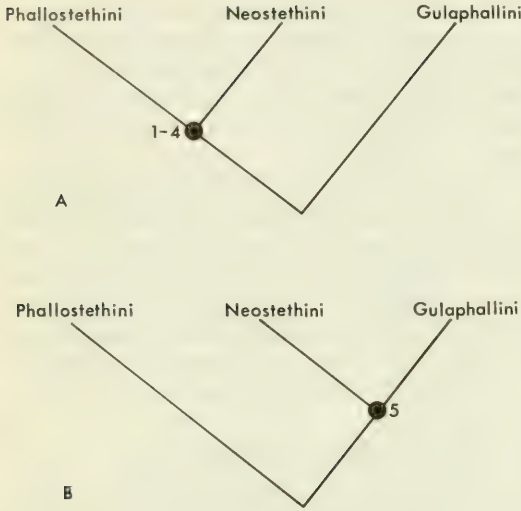


FIGURE 7. Two alternative cladograms of relationships among the three phallostethid tribes. Characters numbered as in Phylogenetic Analysis.

I use the following vernacular terms: phallostethins for Phallostethini, neostethins for Neostethini, and gulaphallins for Gulaphallini. To avoid confusion, no vernacular is used for Phallostethinae. Monophyly of each tribe is considered below. Two alternative relationships are: Phallostethini and Neostethini are sister tribes (Fig. 7a); and Neostethini and Gulaphallini are sister tribes (Fig. 7b). I have found no support for the hypothesis that Gulaphallini and Phallostethini are sister tribes; that possible phylogeny will not be discussed further.

The first alternative is supported by at least four derived characters, two of the priapium, one of the oral jaws, and one of the gill arches. Characters have the same numbers as in the cladograms of Figures 7, 8, and 11.

1. Second ctenactinium present (Figs. 2, 3, 9).

The second ctenactinium is a small, curved, externalized priapial bone that may have bony serrations (Regan 1916:fig. 3). It is present in *Neostethus* (Figs. 3, 9) and *Phallostethus*, and is rudimentary in *Phenacostethus* (Fig. 2). The bone is absent in *Gulaphallus* (Fig. 4), contrary to Aurich (1937) who misidentified the large, partially externalized papillary bone as a second ctenactinium.

2. Shieldlike pulvinulus present (Figs. 2, 9) and outer pulvinular bone robust (Figs. 2, 3).

The oval pulvinulus of *Phallostethus*, *Phena-*

costethus (Fig. 2), and *Neostethus* (Fig. 9) forms a shieldlike covering of the articulation point between the outer pulvinular and proctal axial bones. The outer pulvinular bone, although present in gulaphallins (Fig. 4), is larger and more robust in phallostethins and neostethins. Bailey (1936) and Aurich (1937) reported a slender, long pulvinulus paralleling the longitudinal ctenactinial muscles in *Gulaphallus*. However, the structure in *Gulaphallus* appears to be simply a fold of skin covering the muscles and is viewed here as doubtfully homologous with the distinctive pulvinulus of neostethins and phallostethins.

3. Highly protrusible oral jaws.

Premaxillary ascending processes are long, and a short, rodlike block (submaxillary element of Parenti 1984) lies between the maxilla and vomer in Neostethini and Phallostethini, both characters contributing to the highly protrusible oral jaws (Roberts 1971b; Ivantsoff et al. 1987). The block may be ossified in *Phallostethus* and some species of *Neostethus*; otherwise it is cartilaginous. In Gulaphallini, there is a thin connective tissue meniscus between the maxilla and vomer, except in *G. panayensis* in which the meniscus is enlarged.

4. Reduction of hyobranchial apparatus.

The entire hyobranchial apparatus is reduced in phallostethids relative to other atherinoids (see Rosen and Parenti 1981). Teeth on the fourth ceratobranchial toothplate are few or absent in phallostethins and neostethins; they are present in outgroup taxa such as *Dentatherina merceri* and *Pseudomugil signifer*, as well as in *Gulaphallus*.

The alternative that Neostethini and Gulaphallini are sister tribes is supported by what may be described as one complex priapial character.

5. Anterior elongation of priapial suspensory system, including anteriorly expanded cleithra and transverse processes of fourth vertebrae of males, with the proctal transverse process larger than the slightly modified aproctal transverse process (Figs. 3, 4), and elongate first ctenactinium, the prominent externalized priapial bone (Figs. 3, 4, 9).

Parsimony may be used to choose the first phylogenetic hypothesis (Fig. 7a) over the second (Fig. 7b), but that criterion alone is not satisfactory. Outgroup comparison is of limited use in deciding polarity of priapial structures, and likewise, complex priapial characters may be treated

as one or several characters. I choose the hypothesis that Phallostethini and Neostethini are sister tribes for reasons of parsimony and also because derived characters other than those of the priapium are shared. This hypothesis requires that anterior elongation of the priapium in neostethins and gulaphallins (character 5, above) be viewed as plesiomorphic for all phallostethids.

Monophyly of Tribes

Phallostethini.—Four characters distinguish phallostethins from all other phallostethids.

6. A large, fleshy seminal papilla.

The seminal papilla is enlarged relative to the papilla in neostethins or gulaphallins (Fig. 5). The large papilla may be smooth (Roberts 1971a: fig. 5) or ruffled (Roberts 1971a: fig. 4). An enlarged seminal papilla refutes the hypothesis that the diminutive phallostethins can be described solely as paedomorphic phallostethids.

7. The curved toxactinium the largest externalized bony priapial element (Fig. 2).

Treating the distinctive curved toxactinium as a derived character of *Phallostethus* and *Phenacostethus* is consistent with the interpretation (above) that the elongate ctenactinium and anterior elongation of the priapium in neostethins and gulaphallins are primitive for phallostethids.

8. Extremely small and delicate, with deciduous scales.

The largest phallostethid, *Gulaphallus eximius*, reaches a recorded 37 mm SL (see character 47, below). TeWinkel (1939) gives an unsupported range of 14–40 mm SL. Neostethins and gulaphallins generally mature at over 20 mm SL; the exception, *N. borneensis*, is considered secondarily reduced. Small adult size and the deciduous scales of phallostethins are probably paedomorphic characters correlated with character 9.

9. A translucent, membranous dome on dorsal surface of head.

The membranous dome (Roberts 1971a: figs. 2, 3) on the dorsal surface of the head may best be described as a larval characteristic of atherinoids (as in *Hypoatherina bleekeri*; see Takita and Nakamura 1986) retained in adults.

Neostethini.—Two characters distinguish *Neostethus* from all other phallostethids.

10. An inner pulvinular bone (Fig. 3).

The inner pulvinular bone is a large, well-developed chondral bone lying just posterior to, and articulating with, the outer pulvinular bone. It has no identified homolog in phallostethins or gulaphallins.

11. A high number of thin, bony projections on the papillary bone (Fig. 3).

The papillary bone has a high number (reportedly more than 80; Roberts 1971b) of thin, bony projections in *Neostethus* (Aurich 1937: fig. 6). These are the projections used by Myers (1935) to diagnose a new genus, *Plectrostethus* (= *Neostethus*, herein). Myers apparently compared his new species with phallostethins and gulaphallins, which lack projections. In the neostethins, *Neostethus thessa* and *N. zamboangae*, the papillary bone has only rudimentary projections.

Gulaphallini.—*Gulaphallus* species are together distinguished from all other phallostethids by three derived characters.

12. A perforated gular flap of skin through which the anterior end of the first ctenactinium may pass and remain while at rest (Fig. 5; Aurich 1937: fig. 2).

Neostethins are the other group of phallostethids with an elongate first ctenactinium; however, neostethins do not possess a large gular flap through which the anterior end of the ctenactinium may pass. This character, mentioned and figured by Aurich (1937: fig. 2), is uniquely derived in *Gulaphallus*.

13. The apical axial bone projects beyond ventral body profile (Figs. 4, 5).

In no other phallostethids does a priapial bone project beyond the body profile and away from the body of the priapium.

14. A small, dorsal crest posteriorly on proctal axial bone (Fig. 4).

In other phallostethids (Figs. 2, 3) the proctal axial bone has a uniform dorsal outline.

Species Relationships Within Tribes

Phallostethini

Relationships among, and definitions of, the four phallostethin species *Phallostethus dunckeri*, and *Phenacostethus smithi*, *P. posthon*, and *P. trewavasae* were treated in detail by Parenti (1986a) and need not be repeated here. Defining characters of each species are listed in the Systematic Accounts.

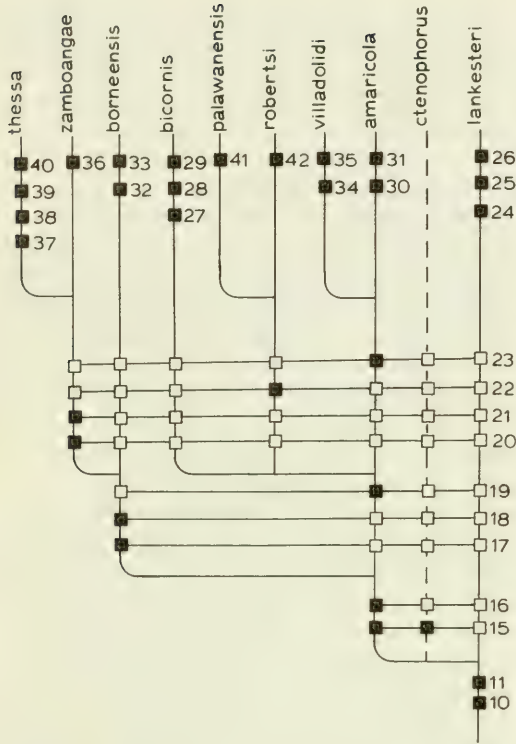


FIGURE 8. Cladogram of relationships among species in the Neostethini. Solid squares, synapomorphies; open squares, symplesiomorphies. Characters numbered as in Phylogenetic Analysis.

Neostethini

Hypothesized relationships among the ten *Neostethus* species are depicted in Figure 8. *Neostethus lankesteri* is considered to be the most plesiomorphic neostethin; it is excluded from a monophyletic group comprising *Neostethus amaricola*, *N. villadolidi*, *N. robertsi*, *N. palawanensis*, *N. bicornis*, *N. borneensis*, *N. zamboangae*, and *N. thessa*, defined by two shared derived characters.

15. An enlarged, prominent, second ctenactinium.

Presence of a second ctenactinium is treated as a derived character of neostethins and phallostethins (see character 1, above). The second ctenactinium is a small curved bone in phallostethins (Fig. 2) and *N. lankesteri* (Fig. 3). It is a much larger, prominent, externalized priapial bone in all other species of *Neostethus*, including *N. ctenophorus*, as illustrated by Aurich (1937: fig. 6). Variation in shape of the second ctenac-

tinium and in its association within other priapial structures is the primary source of information on morphological species recognition within neostethins.

16. A short, bladelike aproctal axial bone.

The aproctal axial bone is nearly as long as the proctal axial bone and reaches the pulvinulus in phallostethins (Fig. 2), *Neostethus lankesteri* (Fig. 3), *N. ctenophorus* (Aurich 1937:fig. 6), and *Gulphallus* (Fig. 4). In all other species of *Neostethus* (Roberts 1971b:fig. 12), the aproctal axial bone is shortened and somewhat bladelike; it does not reach the pulvinulus.

Neostethus ctenophorus, of which no specimens are available, is treated as forming an unresolved trichotomy with *N. lankesteri* and all other *Neostethus* (Fig. 8). I divide these remaining species of *Neostethus* into two monophyletic groups, which I call the *borneensis* and the *bicornis* groups, diagnosed as follows:

The *borneensis* group, comprising *Neostethus borneensis*, *N. thessa*, and *N. zamboangae*, is diagnosed by two shared derived characters that could be treated as one complex priapial character.

17. Strongly curved, thin, second ctenactinium.

The second ctenactinium is a strongly curved, thin bone (Aurich 1937:fig. 4) as opposed to being a stout fin ray as in *Neostethus amaricola* and *N. villadolidi* (Fig. 9) and *N. bicornis* (Roberts 1971b: fig. 12).

18. Papillary and penial bones curved and elongate, lying parallel to dorsal surface of second ctenactinium.

Position of the papillary and penial bones just dorsal to the second ctenactinium means that the seminal papilla (supported by the papillary and penial bones) empties just dorsal to the second ctenactinium, as opposed to a more posterior position in those phallostethids with smaller papillary and penial bones.

The *bicornis* group, comprising *Neostethus bicornis*, *N. palawanensis*, *N. robertsi*, *N. amaricola*, and *N. villadolidi*, is diagnosed by one complex, derived character.

19. Both the proctal and aproctal transverse processes of the fourth vertebra in males are enlarged and oriented anteriorly.

It was concluded (character 5, above) that the anterior elongation of the entire priapial apparatus is a plesiomorphic character for phallostethid fishes. This character complex is modi-

fied in the *bicornis* group such that the aproctal as well as the proctal transverse processes of the fourth vertebra in males are drawn so far anteriorly that the anterior tip of both processes lies parallel to the first vertebra.

Within the *borneensis* group, *Neostethus borneensis* is considered plesiomorphic to *N. thessa* and *N. zamboangae*, diagnosed as sister species by sharing two derived characters.

20. Anterior aproctal ossification present.

In all species of *Neostethus* except *N. lankesteri*, the aproctal axial bone is short and does not reach the pulvinulus (see character 16, above). In *N. thessa* and *N. zamboangae*, there is a thin, elongate ossification just anterior to the aproctal axial bone but separate from it. Aurich (1937: fig. 4) figured the aproctal axial bone and anterior aproctal ossification as one long bone. A similar bone in *N. bicornis* was called the "pulvinular osselet" by Roberts (1971b:fig. 12). However, because of differences in size and shape of the bones, I do not consider that minute ossification in *N. bicornis* to be homologous with the ossification in *N. thessa* and *N. zamboangae*.

21. Reduction in number of papillary projections.

The thin, elongate papillary and penial bones of the *borneensis* group (character 18, above) are even further reduced within *N. thessa* and *N. zamboangae* so that the fine, bony projections of the papillary bone (Fig. 3) are few or absent.

Within the *bicornis* group, I recognize a trichotomy among *N. bicornis* and two sister-group pairs, *N. palawanensis* and *N. robertsi*, and *N. villadolidi* and *N. amaricola*.

Neostethus palawanensis and *N. robertsi* share one derived character.

22. Claw-shaped, anteriorly bifurcated, second ctenactinium (Fig. 13).

The anterior extent of the second ctenactinium in all other phallostethids that have the bone is either blunt (Fig. 3) or sharply pointed (Fig. 9). Hence, the claw-shaped, anteriorly bifurcated second ctenactinium of *N. palawanensis* and *N. robertsi* (Fig. 13), much larger and better developed in the latter species, is judged to be uniquely derived within phallostethids.

Neostethus villadolidi and *N. amaricola* share one derived character.

23. Sharply pointed second ctenactinium (Fig. 9).

Neostethus villadolidi and *N. amaricola* are two small, narrow-bodied phallostethid species dis-

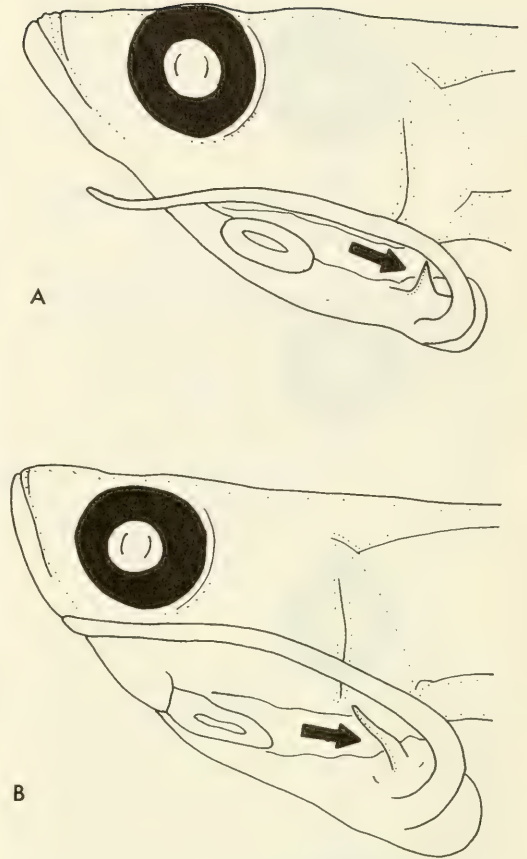


FIGURE 9. Diagrammatic representation of head and anterior portion of body, a. *Neostethus villadolidi*, sinistral male, CAS 60258, b. *Neostethus amaricola*, sinistral male, CAS-SU 38898. Anterior to left. Arrow points to second ctenactinium.

tinguished from all other phallostethids by their sharply pointed, either anteriorly or dorsally directed, second ctenactinia.

Autapomorphies of Each Species of *Neostethus*

Neostethus lankesteri

24. Males with a small, slightly pointed, triangular, ventral bony projection on the elongate first ctenactinium (Fig. 3).

The first ctenactinium is an elongate, uniformly rod-shaped bone in all other phallostethids in which it occurs. *Neostethus lankesteri* is unique among phallostethids in having a small, slightly pointed, triangular, bony projection on the ventral surface of the first ctenactinium (Fig. 3).

25. Distal tips of the first pleural ribs project beyond ventral outline of priapium.

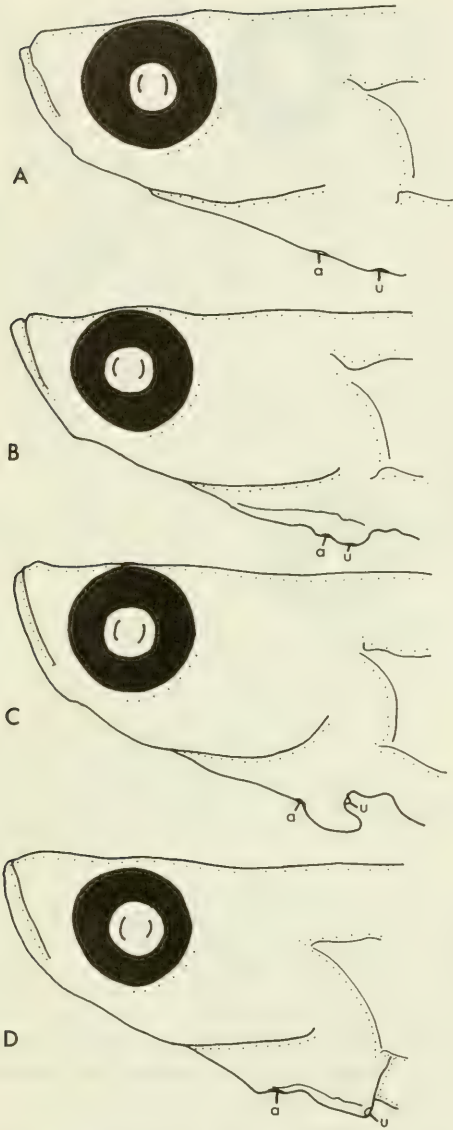


FIGURE 10. Diagrammatic representation of head and anterior portion of body, adult female, a. *Neostethus thessa* (CAS-SU 36546), b. *Neostethus villadoloidi* (CAS 60258), c. *Neostethus lankesteri* (CAS-SU 67162), d. *Neostethus bicornis* (CAS 35783). Abbreviations: a, anus; u, urogenital opening.

The first pleural ribs in all phallostethid males are offset to the proctal side of the priapium (Fig. 3). In *N. lankesteri*, the distal tips of the ribs project beyond the ventral outline of the priapium when it is viewed from the proctal side.

26. Females have a large, hooklike, urogenital papilla (Fig. 10c).

In all female phallostethids, the anus is ante-

rior to the urogenital openings (Fig. 10). Most species are like *N. thessa* (Fig. 10a), in which females have no anal or urogenital papilla or covering. Adult female *N. lankesteri* are readily distinguished from all other phallostethid females by a large, hooklike papilla that lies posterior to the anal opening and anterior to the urogenital openings, towards which it curves (Fig. 10c).

Neostethus bicornis

27. Mature males with two, elongate ctenactinia.

The second ctenactinium of *N. bicornis* is the longest of any phallostethid, at least one-half the length of the first ctenactinium in adult males (Roberts 1971b:fig. 12).

28. Immature males with a brown blotch on the proctal pelvic rays that fades with growth and maturity.

Immature males can be readily identified as sinistral or dextral (see Parenti 1986a and character 44, below) by a small brown blotch present on the proctal pelvic fin rays. This blotch becomes diffuse, hence less recognizable, with growth.

29. Females with a fleshy, hoodlike flap covering the urogenital openings (Fig. 10d).

Adult female *N. bicornis* are readily distinguished from all other phallostethids by the presence of a unique fleshy, hoodlike flap that extends from the anus to the urogenital openings (Fig. 10d). Although females of *N. lankesteri* and *N. bicornis* have fleshy coverings of the urogenital openings, I do not recognize this as a shared derived character because form of the urogenital covering is different in the two species, and numerous other characters refute a close relationship between the two.

Neostethus amaricola

30. Distal tips of the first pleural ribs of females project beyond the ventral body profile.

Herre (1942:148) used "Female with two spurs or papillae on sides of throat" as a key character of *N. amaricola*. The spurs or papillae are the distal tips of the first pleural ribs that project beyond the ventral body profile on either side of the urogenital openings.

31. A sharply pointed, anteriorly directed, second ctenactinium (Fig. 9b).

Males of *N. amaricola* are readily distin-

guished from those of its sister species, *N. villadolidi*, by a sharply pointed second ctenactinium that is directed anteriorly (Fig. 9).

Neostethus borneensis

Neostethus borneensis is a relatively short-bodied species that is distinguished from all other neostethins by two, probably correlated, characters (see *G. panayensis*, below, for a similar definition).

32. Low number of vertebrae (31–32) (Table 2) in males and females.

Vertebrae in other species of *Neostethus* range from 34 to 37 (Table 2), in *Gulaphallus* from 35 to 37, except for *G. panayensis* in which the number of vertebrae is also reduced, and in phallostethins from 33 to 40 (Table 2). Vertebrae number 40–43 in *Dentatherina merceri* (fide Patten and Ivantsoff 1983:332), and 29–30 in *Pseudomugil signifer* (CAS 62565), two outgroup species. The plesiomorphic vertebral number for phallostethids is ambiguous. I treat the vertebral number in *N. borneensis* as derived because it is low compared to all other neostethins and phallostethins.

33. Low number of scales in a lateral series (25–27) (Table 2) in males and females.

Scales in a lateral series in other species of *Neostethus* range from 29 to 34, and in *Gulaphallus* from 28 to 58 (Table 2). Scales in a lateral series number 40–43 in *Dentatherina merceri* (fide Patten and Ivantsoff 1983:332), and 29–32 in *Pseudomugil signifer* (CAS 62565), two outgroup species. The plesiomorphic number of scales in a lateral series in phallostethids is ambiguous. I hypothesize that the number in *N. borneensis* is derived because it is low compared to outgroup species and other phallostethids.

Neostethus villadolidi

34. A fleshy urogenital protuberance (Fig. 10b) in females.

Adult female *N. villadolidi* have a fleshy protuberance just posterior to the anus and anterior to the urogenital openings. It could be described as an incipient or rudimentary papilla; however, I do not recognize a transition series from the state of the urogenital papilla in *N. lankesteri* or the urogenital flap in *N. bicornis*, as discussed above for character 29.

35. A sharply pointed, dorsally directed second ctenactinium (Fig. 9a).

Male specimens of *N. villadolidi* are readily distinguished from male specimens of *N. amari-cola*, its proposed sister species, by a sharply pointed second ctenactinium that is directed dorsally (Fig. 9).

Neostethus zamboangae

36. A small, hooked, second ctenactinium with two to seven bony serrations.

Neostethus zamboangae adult males have two to seven bony serrations on the ventral surface of the hooked second ctenactinium. Regan (1913: figs. 1, 3) illustrated serrations on what I identify as the second ctenactinium in *Phallostethus dunckeri*; however, I do not propose a close relationship between *N. zamboangae* and *P. dunckeri* because other characters lead me to conclude that they are members of different, monophyletic tribes.

Neostethus thessa

37. Absence of first dorsal fin rays and most of the first dorsal pterygiophore in males and females.

The first dorsal fin is absent in three phallostethid species: *N. thessa*, *Phallostethus dunckeri* (Parenti 1986a), and *Gulaphallus bikolanus*. I view this absence as the individual loss of the first dorsal fin in each species. A first dorsal fin is plesiomorphic for atherinomorphs, being present in outgroups *Bedotia*, *Melanotaenia*, *Hypopotherina*, *Dentatherina*, and *Pseudomugil* and all other phallostethids. Each of the three phallostethid species that lacks a first dorsal fin is a member of its own well-corroborated monophyletic group, and a remnant of the first dorsal pterygiophore is present in some specimens.

38. Oral dentition reduced to several small unicuspid teeth on premaxilla and dentary in males and females.

Oral teeth, in one or two rows in other *Neostethus* species, are reduced to a few randomly distributed unicuspid teeth in *N. thessa*.

39. A relatively long anal fin (17–22 rays) (Table 2) in males and females.

Anal fin rays in other *Neostethus* and *Gulaphallus* number from 13 to 18 (Table 2), in *Phenacostethus* from 14 to 15 (Table 2). *Phallostethus dunckeri* is the one other phallostethid species having a relatively long anal fin with 26–28 rays (Table 2). In one outgroup species, *Dentatherina*

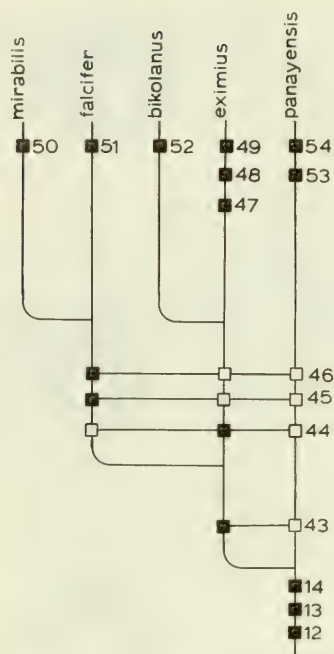


FIGURE 11. Cladogram of relationships among species in the Gulaphallini. Solid squares, synapomorphies; open squares, symplesiomorphies. Characters numbered as in Phylogenetic Analysis.

merceri, anal fin rays number from 15 to 17 (Patten and Ivantsoff 1983).

40. A relatively long second dorsal fin (8–10 rays) (Table 2) in males and females.

Second dorsal fin rays in other *Neostethus* range from 5 to 7, in *Gulaphallus* from 6 to 8, in *Phenacostethus* from 5 to 7, and in *Phallostethus*, 8–10 (Table 2). Absence of the first dorsal fin and increase in the number of second dorsal fin rays in both *N. thessa* and *P. dunckeri* invites speculation that the two dorsal fins have become confluent in development. However, absence of the first dorsal fin in *Gulaphallus bikolanus* with no increase in number of second dorsal fin rays refutes this as a general phenomenon in phallostethids.

Neostethus palawanensis

41. A relatively straight first ctenactinium with a broad, fleshy ventral ridge.

The first ctenactinium is the prominent externalized priapial bone in neostethins and gulaphallins (see character 5, above). It is typically a

long, slender, curved bone (Figs. 3, 4) except in *N. palawanensis* in which it is relatively straight and has a thick, fleshy ventral ridge (Myers 1935). I consider the fleshy ventral ridge uniquely derived in *N. palawanensis*.

Neostethus robertsi

42. A large, well-developed, claw-shaped second ctenactinium (Fig. 12).

Neostethus robertsi and *N. palawanensis* are considered sister species because they share the uniquely derived character of a claw-shaped, anteriorly bifurcated, second ctenactinium (see character 22, above). The claw-shaped second ctenactinium is much larger and better developed in *N. robertsi* than in *N. palawanensis*.

Neostethus ctenophorus

There are no identifiable autapomorphies of *N. ctenophorus* (see Systematic Accounts).

Gulaphallini

Relationships among the five *Gulaphallus* species are depicted in Figure 11. Four species, *G. eximius*, *G. mirabilis*, *G. falcifer*, and *G. bikolanus*, are considered to be most closely related because they share one derived character.

43. Large, well-developed aproctal axial bone (Fig. 4).

The aproctal axial bone is relatively large and has a well-developed dorsal and ventral ridge in *G. eximius*, *G. mirabilis*, *G. falcifer*, and *G. bikolanus* (Fig. 4), as opposed to the condition in *G. panayensis* in which the bone is thin and elongate.

Gulaphallus bikolanus and *G. eximius* are considered sister species because they share one derived character.

44. Adult males exclusively dextral.

All adult male phallostethids are bilaterally asymmetric: a sinistral male has the seminal papilla offset to the left side of the body and the anus offset to the right (Parenti 1986a). The reverse is true for dextral males. Sinistral and dextral males occur in about equal numbers in all phallostethid species except the sister species *Phenacostethus trewavasae*, which is sinistral, *Phenacostethus posthon*, which is dextral, and the two species of *Gulaphallus*. I (Parenti 1986a) reviewed the phenomenon of bilateral asymmetry

in phallostethids and speculated that the *Phenacostethus* sister species evolved from an ancestral species in which there were both sinistral and dextral males and concluded that such statements of ancestry are untestable. My hypothesis that *G. eximius* and *G. bikolanus* are sister species because males of each are exclusively dextral does not refute this argument about speciation. The proposal requires that the common ancestor of the two *Gulaphallus* species was exclusively dextral. If that ancestral species had an exclusively sinistral sister species, it is unknown to us now.

Gulaphallus mirabilis and *G. falcifer* are considered to be sister species because they share two derived characters.

45. Antepleurale element ossified in males and females.

The antepleurale cartilage surrounds the distal tips of the first pleural ribs. It is ossified in *G. mirabilis* and *G. falcifer* and cartilaginous in other species of *Gulaphallus*.

46. A brown blotch (concentration of melanophores) at midventral surface just anterior to anal fin in males and females.

Parenti (1986b) used this pigmentation pattern as an identifying character of *G. falcifer*. However, it is found also in *G. mirabilis* and hence used as a derived character to support a close relationship between the two species.

Autapomorphies of Each Species of *Gulaphallus*

Gulaphallus eximius

47. Relatively large body size and scales in a lateral series more than 50 (range 52–58) (Table 2) in males and females.

Gulaphallus eximius is the largest known phallostethid, reaching a recorded 37 mm SL (Herre 1942). Although large size may be considered plesiomorphic for phallostethids, *G. eximius* is perhaps best described as secondarily large. One possible sister taxon, *Dentatherina merceri*, is relatively small, maturing at under 25 mm SL (Patten and Ivantsoff 1983). Correspondingly, *G. eximius* has a high number of scales in a lateral series, ranging from 52 to 58, as opposed to a range of 25–34 for all other neostethins and gulaphallins except *G. mirabilis* (see character 50, below). Also, outgroup species, *D. merceri* and *Pseudomugil signifer* have fewer scales than does *G. eximius* (see character 33, above).

48. A brown blotch (concentration of melanophores) surrounds the anus and urogenital openings in immature females.

This pigmentation pattern is not found in other phallostethids nor in outgroup species and, therefore, is considered uniquely derived in *G. eximius*.

49. Rudimentary pelvic girdle represented by two small scale-like discs of bone in adult females.

Just posterior to the urogenital openings in females is a pair of ossified discs inferred to be a rudimentary pelvic girdle. Similar pelvic girdle elements are found in adult female *Phenacostethus posthon* (see Parenti 1986b:fig. 4).

Gulaphallus mirabilis

50. Scales in lateral series range from 36 to 38 (Table 2).

The high number of scales in a lateral series in *G. mirabilis* is judged to be an independent increase (see character 47, above).

Gulaphallus falcifer

51. Adult females with an elongate pelvic fin ray projecting beyond body profile on either the left or right side of the urogenital opening.

Parenti (1986b) described development of the elongate asymmetric bony element in females of *G. falcifer*, concluding that it is homologous with a pelvic fin ray, not a postcleithrum. *Gulaphallus falcifer* is the only phallostethid in which bilateral asymmetry has been described in females.

Gulaphallus bikolanus

52. First dorsal fin absent in males and females.

Absence of the first dorsal fin in *G. bikolanus* is hypothesized to be independent of its absence in *N. thessa* and *P. dunckeri* (see character 37, above) for reasons of parsimony.

Gulaphallus panayensis

Gulaphallus panayensis is a relatively small *Gulaphallus* species defined by two, probably correlated, characters (see *N. borneensis*, above, for a similar definition).

53. A low number of vertebrae (31–33) (Table 2) in males and females.

The low number of vertebrae in *G. panayensis* is considered a reduction from a higher, plesio-morphic number for phallostethids (see character 32, above).

54. A low number of scales in a lateral series (28–30) (Table 2) in males and females.

The low number of scales in a lateral series is considered a reduction from a higher, plesio-morphic number for phallostethids (see character 33, above).

KEY TO PHALLOSTETHIDAE

The following key is based primarily on characters discussed in the Phylogenetic Analysis. However, characters used to identify the species of *Phallostethus* and *Phenacostethus* are from Parenti (1986a).

- 1A. Second ctenactinium present (Figs. 2, 3, 9); shieldlike pulvinulus present (Figs. 2, 9); outer pulvinular bone robust (Figs. 2, 3); oral jaws highly protrusible; few or no teeth on fourth ceratobranchial toothplate; no perforation in skin of gular region; aproctal axial bone does not project beyond ventral body profile; no dorsal crest on proctal axial bone *Phallostethinae* 2A
- 1B. No second ctenactinium; no pulvinulus; outer pulvinular bone small; oral jaws not highly protrusible; teeth on fourth ceratobranchial toothplate; perforated gular flap of skin through which anterior end of first ctenactinium may pass (Fig. 5); aproctal axial bone projects beyond ventral body profile (Figs. 4, 5); small, dorsal crest posteriorly on proctal axial bone (Fig. 4) *Gulaphallini* 15A
- 2A. Large, fleshy, smooth or ruffled, seminal papilla; large, externalized, curved toxactinium; translucent, membranous dome on dorsal surface of head; no inner pulvinular bone; no bony projections on papillary bone *Phallostethini* 3A
- 2B. Seminal papilla small; no externalized toxactinium; no translucent, membranous dome on dorsal surface of head; inner pulvinular bone present (Fig. 3); high number of thin, bony projections on papillary bone (Fig. 3) or just rudimentary projections *Neostethini* 6A
- 3A. Anal fin rays 26–28; vertebrae 40; second ctenactinium serrated; oral jaws equal; no first dorsal fin; second dorsal fin rays 8–10 *Phallostethus dunckeri* (p. 267)
- 3B. Anal fin rays 14–15; vertebrae 33–35; second ctenactinium greatly reduced and not serrated; lower oral jaw projects beyond upper oral jaw; first dorsal fin ray 1; second dorsal fin rays 5–7 *Phenacostethus* 4A
- 4A. Distal end of seminal papilla ruffled; slightly curved toxactinium (Fig. 2), penial bone present *Phenacostethus smithi* (p. 268)
- 4B. Distal end of seminal papilla smooth; greatly curved toxactinium; penial bone absent 5A
- 5A. First dorsal fin origin posterior to base of last anal fin ray; males dextral; eye-lens large *Phenacostethus posthon* (p. 268)
- 5B. First dorsal fin origin opposite midpoint of anal fin; males sinistral; eye-lens small to minute *Phenacostethus trewavasae* (p. 268)
- 6A. Second ctenactinium small; small, slightly pointed, ventral bony projection on elongate first ctenactinium (Fig. 3); posterior tips of first pleural ribs project beyond body of priapium; females with large, hooklike genital papilla (Fig. 10c) *Neostethus lankesteri* (p. 269)
- 6B. Second ctenactinium large; ventral margin of first ctenactinium smooth, no pointed projection; posterior tips of first pleural ribs do not project beyond body of priapium; females with urogenital papilla that may be fleshy but does not form distinct hook 7A
- 7A. Long aproctal axial bone, reaches pulvinulus *Neostethus ctenophorus* (p. 272)
- 7B. Short, bladelike aproctal axial bone, does not reach pulvinulus 8A
- 8A. Strongly curved, thin, second ctenactinium; papillary and penial bones curved and elongate, lying parallel to dorsal surface of second ctenactinium; proctal transverse processes of fourth vertebra of males enlarged and oriented anteriorly *borneensis* group 9A
- 8B. Straight, stout, second ctenactinium; papillary and penial bones short and straight; proctal and aproctal transverse processes of fourth vertebra of males en-

- larged and oriented anteriorly
..... *bicornis* group 11A
- 9A. Anterior aproctal ossification present; few or no bony projections on papillary bone; vertebrae 35–37; scales in lateral series 29–34 10A
- 9B. No anterior aproctal ossification; numerous bony projections on papillary bone; vertebrae 31–32; scales in lateral series 25–27
..... *Neostethus borneensis* (p. 270)
- 10A. Small, hooked, second ctenactinium with 2–7 bony serrations; first dorsal fin rays 2; second dorsal fin rays 5–6; complete row of teeth on premaxilla and on dentary; anal fin rays 15–17
..... *Neostethus zamboangae* (p. 271)
- 10B. Small, hooked second ctenactinium with no bony serrations; no first dorsal fin; second dorsal fin rays 8–10; several small unicuspid teeth on premaxilla and on dentary; anal fin rays 17–22
..... *Neostethus thessa* (p. 272)
- 11A. Mature males with two elongate ctenactinia; immature males with brown blotch on proctal pelvic rays; females with fleshy, hoodlike flap covering urogenital openings (Fig. 10d)
..... *Neostethus bicornis* (p. 269)
- 11B. Mature males with one elongate ctenactinium; immature males with clear pelvic rays; urogenital openings of females exposed, not covered by fleshy, hoodlike flap 12A
- 12A. Claw-shaped, anteriorly bifurcated, second ctenactinium 13A
- 12B. Sharply pointed second ctenactinium (Fig. 9) 14A
- 13A. Straight first ctenactinium with broad, fleshy, ventral ridge; small, claw-shaped second ctenactinium
..... *Neostethus palawanensis* (p. 271)
- 13B. Slightly bowed first ctenactinium with smooth ventral outline, no fleshy ridge; large, claw-shaped second ctenactinium (Fig. 13) *Neostethus robertsi* (p. 272)
- 14A. Distal tips of first pleural ribs of females project beyond ventral body profile; sharply pointed, anteriorly directed second ctenactinium (Fig. 9b); no fleshy protuberance anterior to urogenital openings of females
..... *Neostethus amaricola* (p. 270)
- 14B. Distal tips of first pleural ribs of females do not project beyond ventral body profile; sharply pointed, dorsally directed second ctenactinium (Fig. 9a); fleshy protuberance anterior to urogenital openings in females (Fig. 10b)
..... *Neostethus villadolodi* (p. 271)
- 15A. Thin, elongate aproctal axial bone; vertebrae 31–33; scales in lateral series 28–30 *Gulaphallus panayensis* (p. 275)
- 15B. Large, well-developed aproctal axial bone (Fig. 4); 35–37 vertebrae; scales in lateral series 32 or more 16A
- 16A. Males dextral; antepleuralelement cartilaginous in adults; midventral surface with tiny, scattered melanophores . . 17A
- 16B. Males sinistral or dextral; antepleuralelement ossified in adults; brown blotch at midventral surface just anterior to anal fin 18A
- 17A. Scales in lateral series 52–58; brown blotch surrounds anus and urogenital openings in immature females; rudimentary pelvic girdle represented by two small scalelike discs of bone in adult females; first dorsal fin present with rays 1–2 *Gulaphallus eximius* (p. 274)
- 17B. Scales in lateral series 32; anus and urogenital openings in females surrounded by tiny, scattered melanophores; no rudimentary pelvic girdle in adult females; no first dorsal fin
..... *Gulaphallus bikolanus* (p. 275)
- 18A. Scales in lateral series 36–38; pelvic rays do not project beyond ventral body profile *Gulaphallus mirabilis* (p. 274)
- 18B. Scales in lateral series 32; an elongate pelvic fin ray projecting beyond body profile on either the left or right side of urogenital opening in adult females ...
..... *Gulaphallus falcifer* (p. 274)
- CLASSIFICATION OF PHALLOSTETHIDAE
- The following classification of phallostethids reflects some conclusions of the Phylogenetic Analysis. All higher taxa are monophyletic. Species are listed in order of year of description.
- Family Phallostethidae Regan, 1913
Subfamily Phallostethinae Regan, 1913
Tribe Phallostethini new status
Genus *Phallostethus* Regan, 1913
P. dunckeri Regan, 1913

CLASSIFICATION OF PHALLOSTETHIDAE

The following classification of phallostethids reflects some conclusions of the Phylogenetic Analysis. All higher taxa are monophyletic. Species are listed in order of year of description.

Family Phallostethidae Regan, 1913

Subfamily Phallostethinae Regan, 1913

Tribe Phallostethini new status

Genus *Phallostethus* Regan, 1913

P. dunckeri Regan, 1913

Genus *Phenacostethus* Myers, 1928*P. smithi* Myers, 1928*P. posthon* Roberts, 1971*P. trewavasae* Parenti, 1986

Tribe Neostethini new status

Genus *Neostethus* Regan, 1916*N. lankesteri* Regan, 1916*N. bicornis* Regan, 1916*N. palawanensis* (Myers, 1935), new combination*N. amaricola* (Villadolid and Manacop, 1935)*N. thessa* (Aurich, 1937), new combination*N. ctenophorus* (Aurich, 1937), new combination*N. borneensis* Herre, 1939*N. villadolidi* Herre, 1942*N. zamboangae* Herre, 1942*N. robertsi* new species

Subfamily Gulaphallinae Aurich, 1937

Tribe Gulaphallini new status

Genus *Gulaphallus* Herre, 1925*G. eximius* Herre, 1925*G. mirabilis* Herre, 1925*G. bikolanus* (Herre, 1926), new combination*G. falcifer* Manacop, 1936*G. panayensis* (Herre, 1942), new combination

SYSTEMATIC ACCOUNTS

Family Phallostethidae Regan, 1913

Type genus *Phallostethus* Regan, 1913

Phallostethinae Regan, 1913 (as subfamily of Cyprinodontidae)

Neostethinae Aurich, 1937 (as subfamily of Phallostethidae, type genus *Neostethus* Regan)Gulaphallinae Aurich, 1937 (misprinted Gulaphalinae, as subfamily of Phallostethidae, type genus *Gulaphallus* Herre)

DIAGNOSIS.—Small to minute, laterally compressed, nearly transparent, atherinomorph fishes, largest size recorded 37 mm SL. Anus and urogenital openings anterior, below pectoral fin base, in both sexes. A median, abdominal, slightly frayed, fleshy ridge or keel from urogenital openings to anterior rays of anal fin. First dorsal fin with one or two short spines or thickened rays, or no rays but pterygiophore may be present.

Copulatory organ of males a priapium. The following characters are of males, unless other-

wise noted. Main bony priapial support the proctal axial bone. Main externalized bone(s) a toxactinium, a toxactinium and a ctenactinium, or one or two ctenactinia. Anterior ramus of cleithrum elongate anteriorly or not. Postcleithra absent or present as small slivers of bone in both sexes. First pair of pleural ribs expanded anteroposteriorly and dorsoventrally, ventral tips meeting and enclosed in block of cartilage and/or bone, the antepleural element. Large, fibrous pad, the pulvinulus, if present, covers point of articulation of toxactinium, proctal axial bone, and anterior extent of cleithra. Fertilization internal, sperm bundles passed to females through seminal papilla, which may be large or small, smooth or ruffled, and supported internally by papillary and penial bones. Development oviparous; females lay fertilized eggs.

Males bilaterally asymmetric: anus and seminal papilla offset to opposite sides of body, proctal and aproctal, respectively. Prominent externalized priapial bones arise on left or right side of body. Proctal, or proctal and aproctal, transverse processes of fourth vertebrae expanded and oriented anteriorly or not. Females bilaterally symmetric except those of *Gulaphallus falcifer*, in which one pelvic ray is enlarged on either left or right side of body at urogenital openings. Pelvics otherwise absent or represented by bundle of fin rays, called fringe, surrounding epididymis. Small postanal papillae may contain rudimentary pelvic girdles and rays in adult female *Phenacostethus posthon* and *Gulaphallus eximius*.

Hyobranchial apparatus with reductions from typical atherinoid condition; teeth on fourth ceratobranchial toothplate present or absent. Branchiostegal rays 4 to 6.

DESCRIPTION.—Background uniformly pale yellow or straw-colored in alcohol, with small, dark melanophores on dorsal surface of head and body, midlateral intermuscular septum, along anal fin base, dorsal and ventral midline. Seminal papilla and externalized bones of priapium may be covered with scattered melanophores. Scales cycloid, relatively small to medium-sized, and deciduous. Dorsal scales with faint dark margins. Eye-lens large to minute. Dorsal surface of head with translucent, membranous dome or not. Mouth slightly to highly protractile with thin or no meniscus, cartilaginous rod, or ossified submaxillary element between maxilla and vomer. Unicuspid teeth in single or double row, with large teeth on lateral ramus of premaxilla, or few,

small teeth. Second dorsal fin with 5–10 rays. Anal fin unmodified, with 13–28 rays. Pectoral fin with 9–13 rays. Caudal fin emarginate, forming incipient lobes. Caudal skeleton with two epurals, autogenous parhypural, and dorsal and ventral hypural plate. Vertebrae 31–40.

REMARKS.—Regan (1913, 1916), Myers (1928), Bailey (1936), Herre (1942), and Roberts (1971b) listed both diagnostic and descriptive characters of phallostethid fishes. This diagnosis, like the ones that follow, is phylogenetic, as in Weitzman and Fink (1985) for genera of xenurobryconin characid fishes. Only characters or character states hypothesized to be derived are considered diagnostic of taxa. Comparisons among characters used to diagnose species, tribes, and subfamilies are given in the Phylogenetic Analysis and differential diagnoses.

Subfamily Phallostethinae Regan

DIAGNOSIS.—Priapium with a reduced second ctenactinium, and a prominent, shieldlike pulvinulus covering articulation point of robust toxactinium and proctal axial bone. Jaws of males and females highly protrusible with elongate premaxillary ascending processes and distinct submaxillary cartilages or bones, and a reduced hyobranchial apparatus with few or no teeth on fourth ceratobranchial toothplate.

COMPOSITION.—Two tribes, Phallostethini and Neostethini, both family-group names used for the first time at the tribal level.

Tribe Phallostethini new status

DIAGNOSIS.—Males with a large, fleshy seminal papilla that may be smooth or ruffled; toxactinium relatively straight to curved. Adults of both sexes extremely small and delicate, with deciduous scales; a translucent, membranous dome on dorsal surface of head.

COMPOSITION AND DISTRIBUTION.—Two genera, *Phallostethus* Regan from coastal peninsular Malaysia, and *Phenacostethus* Myers, from coastal peninsular Thailand and Malaysia and Sarawak, as diagnosed below.

Genus *Phallostethus* Regan, 1913

Phallostethus Regan, 1913:548–549 (type species: *Phallostethus dunckeri* Regan, 1913 by monotypy).

DIAGNOSIS.—As for *P. dunckeri* Regan, 1913, below.

COMPOSITION AND DISTRIBUTION.—One species from brackish water, mouth of Muar R., Johore, Malaysia (see Roberts 1971a:fig. 1).

Phallostethus dunckeri Regan, 1913

(Fig. 1)

Phallostethus dunckeri Regan, 1913:548–555, figs. 1–4 (original description, mouth of Muar R., Johore, Malay Peninsula); 1916:1, 16–25, figs. 12a, 13–15, pls. 1a, IIIa, IVa, b (characters, comparison with *Neostethus*). Myers 1928:1–6 (characters, comparison with *Phenacostethus*); 1937:137 (characters). Herre 1939:140 (characters). Roberts 1971a:1–20 (relationships). Parenti 1984:1–12, figs. 1–4 (osteology, relationships); 1986a:229–235, tables 1, 2 (relationships, characters); 1986c:41 (characters).

DIFFERENTIAL DIAGNOSIS.—*Phallostethus dunckeri* has an anal fin longer (26–28 rays, as opposed to 13–22) and vertebral number higher (40, as opposed to 31–37) than any other phallostethid. Males are readily separable from those of *Phenacostethus* by a serrated second ctenactinium. Both sexes distinct from *Phenacostethus* by lacking first dorsal fin, and a second dorsal fin with 8–10 rays, rather than 5–7.

MATERIAL.—Lectotype (designated by Ladiges et al. 1958): ZMH 193, dextral ♂, mouth of Muar R., Johore, Malaysia, 1902, G. Duncker, coll. Paralectotypes: BMNH 1913.5.24:18–22 (5 spec.: 1 sinistral ♂, 3 ♀, 1 sex undet.) and ZMH 194–195 (19 spec.: 2 dextral ♂, 14 ♀, 3 juv.), collected with lectotype.

REMARKS.—Ladiges et al. (1958) gave lectotype and paratype (=paralectotype) status to ZMH 193 and 194, respectively. Because ZMH 195 and the BMNH specimens are of the original syntypic series, they are also paralectotypes. Parenti (1986a) called all these specimens syntypes.

Genus *Phenacostethus* Myers, 1928

Phenacostethus Myers, 1928:6 (type species: *Phenacostethus smithi* Myers, 1928 by original designation).

DIFFERENTIAL DIAGNOSIS.—A lower jaw protruding beyond upper jaw and greatly reduced second ctenactinium distinguishes *Phenacostethus* from all other phallostethids. Anal and second dorsal fin rays and vertebrae are fewer than in *Phallostethus*. First dorsal fin with one ray as opposed to first dorsal fin absent in *Phallostethus*.

COMPOSITION AND DISTRIBUTION.—*Phenacostethus smithi* Myers, 1928 and *P. posthon* Roberts, 1971a, in fresh and brackish waters, Thailand and peninsular Malaysia; and *P. trewavasae* Parenti, 1986a, in freshwater, Sarawak, Malaysian Borneo.

Phenacostethus smithi Myers, 1928

(Figs. 1, 2)

Neostethus lankesteri (non Regan). Smith 1927:353–355 (report of specimens from Bangkok, Thailand).

Phenacostethus smithi Myers, 1928:6–8, figs. 1, 2 (original description, Bangkok, Thailand). Smith 1929:14 (characters, distribution). Myers 1937:137–138 (characters). Bailey 1936:470–474, pls. 3, 4 (anatomy, comparison with *Gulaphallus*). TeWinkel 1939:60–68, figs. 1–5 (anatomy, comparison with *Gulaphallus*). Herre 1939:140, 142 (characters, listed). Hubbs 1944:73 (characters). Smith 1945:475–476 (ecology). Roberts 1971a:4–18, figs. 1, 2, 4, 7 (mislabelled as fig. 6) (anatomy, relationships). Parenti 1986a:229–234, fig. 4a, tables 1, 2 (characters, relationships).

Phenacostethus thai Fowler, 1937:219–220, figs. 189, 190 (original description, Bangkok, Thailand).

DIFFERENTIAL DIAGNOSIS.—Unlike other phallostethins, males of *Phenacostethus smithi* have a ruffled, rather than smooth, distal end of enlarged seminal papilla.

MATERIAL.—Holotype: AMNH 9247, dextral ♂, 13.5 mm SL, Bangkok, Thailand, Dec. 1926, H. M. Smith, coll. Paratypes: AMNH 9248 (1 ♀, USNM 92979 (11 spec.: 4 sinistral ♂, 1 dextral ♂, 5 ♀, 1 sex undet.), USNM 202564 (1 ♀, USNM 104417 (1 sinistral ♂), CAS-SU 26520 (8 spec.: 2 sinistral ♂, 3 dextral ♂, 2 ♀, 1 juv.), ANSP 108764 (ex. SU 26520) (2 spec.: 1 dextral ♂, 1 ♀) and USNM 92297 (2 spec.: 1 dextral ♂, 1 ♀), collected with holotype.

Holotype and paratypes of *Phenacostethus thai*: ANSP 51352, ANSP 51353–60 (9 spec.: 2 sinistral ♂, 2 dextral ♂, 5 ♀), Bangkok, Thailand, 2 Aug. 1923, H. M. Smith, coll.

OTHER MATERIAL.—THAILAND: UMMZ 87345 (40 spec.: 10 sinistral ♂, 14 dextral ♂, 15 ♀, 1 juv.), MCZ 47055 (13 spec.: 6 sinistral ♂, 2 dextral ♂, 5 ♀), USNM 93506 (100+), USNM 93507 (50+), USNM 93508 (36 spec.: 5 sinistral ♂, 12 dextral ♂, 17 ♀, 2 juv.), USNM 88668 (100+), USNM 88667 (100+ spec.; 4 juv. cleared and stained), USNM 88659 (3 spec.: 1 sinistral ♂, 1 dextral ♂, 1 ♀), BMNH 1927.12.29:1–10 (31 spec.: 6 sinistral ♂, 4 dextral ♂, 10 ♀, 11 juv.; 2 cleared and stained), ZMA 100.652 (35), and CAS-SU 35957 (112 spec.: 5 cleared and stained), Bangkok, and MCZ 47299 (18 spec.: 1 sinistral ♂, 1 dextral ♂ and 2 ♀ cleared and stained), Chantaburi City. MALAYSIA: USNM 266124 (50+), Trengganu; USNM 266125 (3 spec.: 1 sinistral ♂, 2 ♀), USNM 266126 (15 spec.: 3 sinistral ♂, 5 dextral ♂, 7 ♀), USNM 266127 (1 ♀), Johore.

REMARKS.—In the original description of *Phenacostethus smithi*, Myers (1928:8) stated that “. . . nineteen paratypes, 11 males and 8 females, are deposited in the American Museum of Natural History, the United States National Museum, and my own collection.” I assume that Myers’s “own collection” was deposited, in part, in the Stanford University (SU) collection, now CAS-SU 26520 and ANSP 108764. However, I have no reason to exclude any of the above USNM paratypes of *Phenacostethus smithi* from type status.

In his description of *Phenacostethus thai*, Fow-

lers (1937) did not separate what he called the holotype from other type specimens and I am unable to separate that specimen from the rest of the type material. See also Böhlke (1984:140).

DISTRIBUTION.—Coastal fresh and brackish waters, Thailand and peninsular Malaysia (Roberts 1971a:fig. 1).

Phenacostethus posthon Roberts, 1971

(Fig. 1)

Phenacostethus posthon Roberts, 1971a:12–17, figs. 3, 5, 6 (mislabelled as fig. 7) (original description, Pungah and Langu Town, Thailand). Parenti 1986a:225–235, fig. 5, tables 1, 2 (characters, relationships); 1986b:308–309, figs. 4, 5 (anatomy).

DIFFERENTIAL DIAGNOSIS.—*Phenacostethus posthon* is unique among phallostethins, having a first dorsal fin origin posterior to base of last anal fin ray rather than opposite midpoint of anal fin so that first and second dorsal fins are relatively close together. Males are dextral, as in *Gulaphallus eximius* and *G. bikolanus*, as opposed to sinistral, as in *P. trewavasae*, or sinistral or dextral, as in all other phallostethids.

MATERIAL.—Holotype, MCZ 47300, ♂, 16.7 mm SL, Khlong Kla Soh, about 15 km SW of Pungah Town, Pungah Prov., Thailand, 29 June 1970, T. R. Roberts, coll. Paratypes: MCZ 47301 (2 ♂ cleared and stained), MCZ 47301A (22 ♀), MCZ 47301B (32 ♂), same data as holotype, and MCZ 47302 (20), Khlong Langu at Langu Town, 48 km NW of Satul Town, Thailand, 26 June 1970, T. R. Roberts, coll.

OTHER MATERIAL.—MALAYSIA: USNM 229302 (182 spec.: 82 ♂, 77 ♀, 23 juv.; 6 cleared and stained), Muar R., Johore.

DISTRIBUTION.—Coastal fresh and brackish waters, Thailand and peninsular Malaysia (Roberts 1971a:fig. 1).

Phenacostethus trewavasae Parenti, 1986

(Fig. 1)

Phenacostethus trewavasae Parenti, 1986a:226–229, figs. 1–3, 4b, tables 1, 2 (original description, Baram R., Sarawak, Malaysian Borneo).

DIFFERENTIAL DIAGNOSIS.—*Phenacostethus trewavasae* is unique among phallostethids, having a minute eye-lens, and males sinistral rather than dextral, as in *P. posthon*, *Gulaphallus eximius* and *G. bikolanus*, or sinistral or dextral, as in all other phallostethids.

MATERIAL.—Holotype: ROM 41826, ♂, 14.1 mm SL, Sungei Kejin Tugang, tributary of Sungei Kejin, Baram R., Sarawak, Malaysia, 3 Aug. 1981, D. Watson, coll. Paratypes: ROM 44289 (19), ROM CS812 (3 spec.: 2 ♂, 1 ♀, cleared and stained), ROM 41827 (1), collected with holotype. ROM 41829 (1), ROM

41830 (13), CAS 55454 (5 spec.; 1 cleared and stained), BMNH 1984.7.12:1–5 (5), AMNH 55570 (5), USNM 267266 (5), Sungei Kejin, station at confluence of Kejin Tugang and Kejin R., Baram R., Sarawak, Malaysia, 11 Feb. 1980, D. Watson, coll.

OTHER MATERIAL.—MALAYSIA: ROM 41828 (11), ROM 44290 (29 spec.; 2 ♂ and 2 ♀ cleared and stained) and ROM 44291 (50), Sarawak.

DISTRIBUTION.—Tributaries of Baram R., Sarawak, Malaysian Borneo (Fig. 1).

Tribe Neostethini new status

DIAGNOSIS.—Priapium with an inner pulvinular bone, and thin bony projections numbering 80 or more on papillary bone.

Genus *Neostethus* Regan, 1916

Neostethus Regan, 1916:1, 2 (type species: *Neostethus lankesteri* Regan, 1916 by original designation, use of "gen. et sp. n." for one of two included new species).

Plectrostethus Myers, 1935:5 (type species: *Plectrostethus palawanensis* Myers, 1935, by original designation).

Ceratostethus Myers, 1937:141 (type species: *Neostethus bicornis* Regan, 1916, by original designation).

Solenophallus Aurich, 1937:264 (unavailable; no type species designated of the two treated under genus).

Ctenophallus Herre, 1939:144 (type species: *Solenophallus ctenophorus* Aurich, 1937, by original designation).

Sandakanus Herre, 1942:151 (type species: *Neostethus borneensis* Herre, 1939, by original designation, as a subgenus of *Neostethus* Regan).

Solenophallus Herre (ex Aurich), 1953:242 (type species: *Solenophallus thessa* Aurich, 1937, by original designation).

DIAGNOSIS.—As for the tribe Neostethini, above.

COMPOSITION AND DISTRIBUTION.—Ten species: *N. lankesteri* Regan, 1916, Thailand, peninsular Malaysia, Singapore, and Borneo; *N. bicornis* Regan, 1916, peninsular Malaysia, Singapore, Thailand, Borneo, and Palawan, Philippines; *N. palawanensis* (Myers, 1935), Palawan, Philippines; *N. thessa* (Aurich, 1937), Mindanao, Philippines; *N. ctenophorus* (Aurich, 1937), Luzon, Philippines; *N. borneensis* Herre, 1939, Borneo and Coron, Philippines; *N. zamboangae* Herre, 1942, Mindanao and Luzon, Philippines; *N. robertsi* new species, Luzon, Philippines; *N. amaricola* (Villadolid and Manacop, 1935), and *N. villadolidi* Herre, 1942, throughout Philippines.

Neostethus lankesteri Regan, 1916

(Figs. 1, 3, 10c)

Neostethus lankesteri Regan, 1916:2–14, figs. 1–10, 12B, pls. 1B, 2, 3A, 4C (original description, Muar R., Johore, peninsular Malaysia, and Singapore). Weber and DeBeaufort

1922:381–383, fig. 103 (characters). Myers 1928:8 (characters). Smith 1929:13 (distribution). Myers 1937:139 (listed). Herre 1939:143 (listed). Roberts 1971a:8 (characters). Ivantsoff et al. 1987:651–652, figs. 2A–C, 3A (anatomy, comparisons with atherinoids).

Neostethus siamensis Myers, 1937:139–140 (original description, Chantabun R., Thailand). Herre 1939:143 (listed). Smith 1945:477 (compiled). Roberts 1971a:2–3 (collection report). Parenti 1986c:39–41, fig. 1 (osteology, histology).

Neostethus (*Neostethus*) *lankesteri*. Herre 1942:149 (characters, relationships, distribution).

Neostethus (*Neostethus*) *siamensis*. Herre 1942:150 (characters, probable synonym of *N. lankesteri* Regan).

DIFFERENTIAL DIAGNOSIS.—*Neostethus lankesteri* males can be recognized by a small, slightly pointed, triangular, ventral bony projection on elongate first ctenactinium, and posterior tips of first pleural ribs projecting beyond body of priapium. Females are unique among phallostethids having a large, hooklike, posteriorly projecting, urogenital papilla.

MATERIAL.—Lectotype (here designated): BMNH 1937.12.9:7, dextral ♂, 26.0 mm SL, Muar R., peninsular Malaysia, 18 Feb. 1902, G. Duncker, coll. Paralectotypes: BMNH 1937.12.9:8–10 (3 spec.: 1 dextral ♂, 1 sinistral ♂, 1 ♀) Singapore, G. Duncker, coll. Holotype of *Neostethus siamensis*: USNM 102140, adult ♀, 28.7 mm SL, Chantabun R., Thailand, Apr. 1933, H. M. Smith, coll.

OTHER MATERIAL.—SINGAPORE: BMNH 1970.7.22:71–77 (7 spec.: 1 sinistral ♂, 1 dextral ♂, 5 ♀), R. Tengah; BMNH 1970.7.22:78–79 (2 ♀), R. Serangoon; RMNH 26425 (69 spec.: 22 sinistral ♂, 29 dextral ♂, 18 ♀), R. Berih; CAS-SU 67162 (105 spec.; 5 cleared and stained), R. Selatar. MALAYSIA: FMNH 51653 (1 dextral ♂), East Coast Residency, CAS-SU 61762 (10 spec.: 6 sinistral ♂, 2 dextral ♂, 2 ♀), Sarawak. BRUNEI: CAS-SU 61763 (1). INDONESIA: AMS I.19355–041 (26 spec.: 7 sinistral ♂, 7 dextral ♂, 9 ♀, 3 juv.), East Kalimantan. THAILAND: MCZ 76857 (375 spec.; 6 cleared and stained), near Tha Chalap on road to Chantaburi, Chantaburi Prov.; MCZ 47200 (3), Satul Prov., CAS 63194 (2), Rayong Prov.; CAS 63195 (17), Chumphorn Prov.

DISTRIBUTION.—Coastal localities of Thailand, peninsular Malaysia, Singapore, and Borneo.

Neostethus bicornis Regan, 1916

(Figs. 1, 10d)

Neostethus bicornis Regan, 1916:14–16, fig. 11 (original description, Kuala Langat, peninsular Malaysia). Myers 1928:9 (characters). Herre and Myers 1937:70 (ecology, distribution).

Ceratostethus bicornis (Regan). Myers 1937:141–142 (relationships, referral to new genus). Herre 1939:142 (distribution); 1942:145 (characters, relationships, distribution); 1953:240 (synonymy, distribution). Roberts 1971a:6–10 (characters). Roberts 1971b:397–409, figs. 2–12 (osteology, functional anatomy). Rosen and Parenti 1981:20, fig. 19A (dorsal gill arch anatomy).

DIFFERENTIAL DIAGNOSIS.—Mature males have two elongate ctenactinia rather than a long first ctenactinium and short second ctenactinium as in other *Neostethus*. Immature males have a brown blotch on proctal pelvic fin rays that fades with growth and maturity. Females have a fleshy, hoodlike flap that covers urogenital openings.

MATERIAL.—Lectotype (here designated): BMNH 1937.12.9: 4, immature sinistral ♂, 20.9 mm SL, Kuala Langat, peninsular Malaysia, G. Duncker, coll. Paralectotypes: BMNH 1937.12.9: 5–6 (2 ♀, 16.7–19.1 mm SL), collected with lectotype.

OTHER MATERIAL.—THAILAND: MCZ 47304 (142 spec.; 2 ♀ cleared and stained); MCZ 76856 (71 spec.; 1 sinistral ♂ cleared and stained); MCZ 47305 (93 spec.; 1 dextral ♂ cleared and stained); MCZ 52364 (100+); MCZ 47306 (85 spec.; 1 dextral ♂ and 1 ♀ cleared and stained); MCZ 60081 (70), near Tha Chalap on road to Chantaburi, Chantaburi Prov.; CAS 63196 (2), Chumporn Prov. SINGAPORE: BMNH 1970.7.22: 69–70 (2 spec.: 1 dextral ♂, 1 ♀), R. Poyen; BMNH 1970.7.22: 63–68 (6 spec.: 3 dextral ♂, 3 ♀), R. Tengah; CAS-SU 67161 (10 spec.: 4 sinistral ♂, 5 dextral ♂, 1 juv.), R. Seletar; CAS-SU 35783 (51 spec.; 10 cleared and stained); MNHN 38-14 (4), R. Kranji; CAS-SU 31133 (11 spec.: 9 sinistral ♂, 1 dextral ♂, 1 ♀); USNM 102142 (8 spec.: 1 sinistral ♂, 4 dextral ♂, 3 ♀). BRUNEI: CAS-SU 61764 (1). MALAYSIA: USNM 189012 (5), mangrove swamps on island opposite Sandakan; FMNH 51726–51729 (173), East Coast Residency, Kinabatangan Dist.; and private collection of Maurice Kottelat (5), Sungei Seburut near Matang, Sarawak. PHILIPPINES: USNM 98839 (3) and USNM 150632 (2), Nakoda Bay; USNM 98840 (1), Malam-paya R.; USNM 98838 (3), Palawan. No locality: MCZ 60049 (50+).

DISTRIBUTION.—One of the most widespread phallostethids; coastal localities of Thailand, peninsular Malaysia, Singapore, Borneo, and Palawan, Philippines.

Neostethus amaricola

(Villadolid and Manacop, 1935)

(Figs. 1, 9b)

Gulaphallus amaricola Villadolid and Manacop, 1935:194–196, pl. 1 (original description, Pasay, Rizal Prov., Luzon, Philippines).

Neostethus amaricola (Villadolid and Manacop). Myers 1937: 139 (characters, referral of *G. amaricola* to *Neostethus*). Herre 1939:143 (distribution). Hubbs 1944:73–74 (characters). Herre 1953:241 (distribution).

Neostethus (*Neostethus*) *amaricola*. Herre 1942:149 (characters, relationships, distribution).

DIFFERENTIAL DIAGNOSIS.—Distal tips of first pleural ribs of females of *Neostethus amaricola* project beyond ventral body profile. Males may be recognized by a sharply pointed second ctenactinium directly anteriorly, rather than dorsally as in *N. villadolidi*.

MATERIAL.—PHILIPPINES: USNM 98835 (6 spec.: 1 sinistral ♂, 5 ♀; 13–20 mm SL), Ragay R., Ragay Gulf; FMNH 40771–40785 (15 spec.: 2 sinistral ♂, 5 dextral ♂, 6 ♀, 2 juv.; 13–21 mm SL), Navotas; CAS-SU 32354 (3 spec.: 2 sinistral ♂, 1 ♀; 20–23 mm SL), Nasugbu; CAS-SU 32926 (6 spec.: 1 sinistral ♂, 2 dextral ♂, 3 ♀; 23–24 mm SL), Manila; USNM 98834 (2 spec.: 1 sinistral ♂, 1 dextral ♂), Port San Vicente; USNM 98833 (3 sinistral ♂), Manila Bay; CAS-SU 38898 (200+ spec.; 13 cleared and stained), Navotas; CAS 50724 (266), Nipa creek S. of Masinloc, Luzon. CAS-SU 38899 (190 spec.; 5 cleared and stained), Mindoro.

In the original description, Villadolid and Manacop (1935:195) stated that there were to be at least one male and one female, as well as several additional cotypes collected in Pasay, Rizal Prov., Luzon, in the zoological museum of the College of Agriculture, University of the Philippines. These specimens are presumed lost.

DISTRIBUTION AND REMARKS.—A *Neostethus* species widespread in coastal, brackish-water habitats throughout the Philippines, including Luzon and Mindoro. Herre (1942, 1953) reported *N. amaricola* from Leyte; however, I have reidentified two USNM lots from that locality as the closely related *N. villadolidi*.

Neostethus borneensis Herre, 1939

(Fig. 1)

Neostethus borneensis Herre, 1939:143 (original description, report from around Sandakan Bay, North Borneo); 1940b: 14–17, pls. 10, 11 (description, Kabili R., Sandakan Bay, Segaliud R., North Borneo).

Neostethus (*Sandakanus*) *borneensis*. Herre 1942:151–152 (characters, relationships, distribution); 1953:242 (listed as type species of subgenus *Sandakanus*).

Neostethus (*Sandakanus*) *coronensis* Herre, 1942:152–153 (original description, Coron, Busuanga, Philippines); 1953: 242 (distribution).

Böhlke (1953) followed Herre (1942) in treating Herre's (1940b:14–17) detailed discussion, which included the heading "*Neostethus borneensis*, new species," as the original description. However, Herre's 1940b publication was predated by a compilation and brief statement of identifying characters of phallostethid species (Herre 1939), in which the name, characters, and statement of distribution are recorded. This constitutes the original description of *N. borneensis*.

DIFFERENTIAL DIAGNOSIS.—*Neostethus borneensis* is a robust, relatively short-bodied species with vertebrae (31–32, as opposed to 34–37), and scales in a lateral series (25–27, as opposed to 29–34), fewer than in congeners.

MATERIAL.—Holotype: CAS-SU 33018, sinistral ♂, 16.5 mm SL, Kabili R., Sandakan Dist., North Borneo, 30 Jan. 1937, A. W. C. T. Herre, coll. Paratypes: CAS-SU 33022 (116 ♂; 2 cleared and stained), CAS-SU 33019 (45 ♀), FMNH 51537–51538 (12 spec.: 6 ♂ and 6 ♀). BMNH 1938.12.1:155–164 (19 spec.: 8 ♂, 3 ♀, 8 juv.), collected with holotype. CAS-SU 69021 (7), CAS-SU 69022 (6 cleared and stained), CAS-SU 33020 (9) Segaliud R., North (Malaysian) Borneo, A. W. C. T. Herre, coll. Holotype of *Neostethus coronensis*: CAS-SU 36542, dextral ♂, 22.5 mm SL, Coron, Busuanga, Philippines, 28 June 1940, A. W. C. T. Herre, coll. Paratypes of *N. coronensis*: CAS-SU 36543 (109 spec.: 23 sinistral ♂, 25 dextral ♂, 52 ♀, 9 juv.; 3 cleared and stained) collected with holotype.

OTHER MATERIAL.—MALAYSIA: FMNH 51654 (16), East Coast Residency; USNM 189015 (23), mangrove swamps on island opposite Sandakan.

DISTRIBUTION.—Borneo and Coron, Busuanga, Philippines.

Neostethus villadolidi Herre, 1942

(Figs. 1, 9a, 10b)

Neostethus (Neostethus) villadolidi Herre, 1942:150 (original description, Misamis Oriental, Mindanao, and Negros Oriental, Philippines).

Neostethus villadolidi. Herre 1953:241–242 (distribution).

DIFFERENTIAL DIAGNOSIS.—*Neostethus villadolidi* is a slender-bodied species closely allied with *N. amaricola*, but differing from it and all other phallostethids by having a sharply pointed, dorsally directed, second ctenactinium, and a fleshy urogenital protuberance in females.

MATERIAL.—Holotype: CAS-SU 36537 (misprinted 23637 in original description), sinistral ♂, 22.5 mm SL, mangrove swamp next to Fishery Experiment Station, Cagayan de Misamis, Misamis Oriental Prov., Mindanao, Philippines, 20 Aug. 1940, A. W. C. T. Herre, coll. Paratypes: CAS-SU 36538 (59 spec.: 14 sinistral ♂, 13 dextral ♂, 26 ♀, 6 juv.), collected with holotype.

OTHER MATERIAL.—PHILIPPINES: CAS-SU 52344 (36 spec.: 4 cleared and stained), CAS-SU 36566 (19 spec.: 2 sinistral ♂, dextral ♂, 11 ♀, 5 juv.), and CAS-SU 32355 (111 spec.: 5 sinistral ♂, 31 dextral ♂, 58 ♀, 17 juv.; 7 cleared and stained), CAS 60258 (20 spec.: 10 ♂ and 10 ♀), MNHN 38-15 (4), ROM 54986 (158), ROM 54987 (13), ROM 54988 (80), ROM 50489 (1), ROM 51854 (426), Negros Oriental; AMS I.21938-016 (39), Mactan Island, Cebu; CAS 54645 (12 spec.: 6 dextral ♂, 5 ♀, 1 juv.), northern end of Cuyo, Palawan Prov.; USNM 98836 (1 ♀, 21 mm SL), USNM 98837 (2 spec.: 1 ♀ and 1 dextral ♂), Leyte.

Herre (1942:150) mentioned two lots from Negros Oriental without catalogue numbers, questionably to be included in the description of *N. villadolidi*. I list here several lots from Negros Oriental; however, like Böhlke (1953), I recognize none as type material.

DISTRIBUTION.—Mindanao, Cuyo, Mactan, Negros Oriental and Leyte, Philippines.

Neostethus zamboangae Herre, 1942

(Fig. 1)

Neostethus (Sandakanus) zamboangae Herre, 1942:153–154 (original description, Zamboanga, Mindanao, Philippines); 1953:242 (distribution).

DIFFERENTIAL DIAGNOSIS.—Males of *Neostethus zamboangae* are readily distinguished from congeners by two prominent ctenactinia: an elongate first ctenactinium, and a smaller, hooked second ctenactinium with from two to seven bony serrations. *Phallostethus dunckeri* males also have a serrated second ctenactinium; however, numerous derived characters that distinguish phallostethins from neostethins support a conclusion that these similar second ctenactinia are independently derived.

MATERIAL.—Holotype: CAS-SU 36544, dextral ♂, 22 mm SL, Zamboanga, Mindanao, Philippines, 6 Sep. 1940, A. W. C. T. Herre, coll. Paratypes: CAS-SU 36545 (242 spec.: 30 sinistral ♂, 45 dextral ♂, 117 ♀, 50 juv.; 4 cleared and stained) collected with holotype.

OTHER MATERIAL.—PHILIPPINES: CAS 50725 (141 spec.: 4 cleared and stained); UMMZ 211666 (37), Sorsogon Bay, Buhatan R., 5 km E of Sorsogon Town, Luzon.

DISTRIBUTION.—Coastal localities of Zamboanga, Mindanao and Sorsogon, Luzon, Philippines.

Neostethus palawanensis (Myers, 1935), new combination

(Fig. 1)

Plectrostethus palawanensis Myers, 1935:5–6 (original description, mouth of the Caiholo R., Ulugan Bay, west coast of Palawan, Philippines). Myers 1937:141 (characters). Herre 1939:144 (distribution); 1942:155 (characters, relationships, distribution). Hubbs 1944:71, 73 (characters). Herre 1953:242 (distribution).

Plectrostethus palawensis (misspelling of *P. palawanensis* Myers). Ivantsoff et al. 1987:653–654, fig. 41 (anatomy, comparisons with atherinoids).

DIFFERENTIAL DIAGNOSIS.—*Neostethus palawanensis* is a slender-bodied species readily distinguished by a relatively straight first ctenactinium with a broad, fleshy ventral ridge.

MATERIAL.—Holotype: USNM 93421, sinistral ♂, 22.5 mm SL, mouth of Caiholo R., Ulugan Bay, west coast of Palawan, Palawan Prov., Philippines, 29 Dec. 1908, U.S.S. "Albatross." Paratypes: USNM 93422 (♀, 19 mm SL, allotype = paratype); USNM 93423 (8 spec.: 5 dextral ♂, 3 ♀), collected with holotype.

OTHER MATERIAL.—PHILIPPINES: USNM 93424 (eggs only) collected with holotype and paratypes (no type status). CAS 63200 (17 spec.: 5 sinistral ♂, 4 dextral ♂, 8 ♀; 4 cleared and stained), Cuyo, Palawan Prov.

DISTRIBUTION.—Coastal localities of Palawan and Cuyo, Palawan Prov., Philippines.

Neostethus thessa (Aurich, 1937),
new combination
(Figs. 1, 10a)

Solenophallus thessa Aurich, 1937:264–272, table 1, figs. 1A, 3–5, 7I (original description, Lake Mainit, Mindanao, Philippines). Herre 1939:142 (distribution); 1953:242 (valid description of *Solenophallus*).

DIFFERENTIAL DIAGNOSIS.—*Neostethus thessa* is readily distinguished from congeners by: no dorsal fin rays (remnant of first dorsal pterygiophore present in some specimens); oral dentition reduced to several small, unicuspid teeth on premaxilla and dentary; anal fin with 17–22 rays, as opposed to 13–18; and second dorsal fin with 8–10 rays, as opposed to 5–7.

MATERIAL.—PHILIPPINES: CAS-SU 36546 (46 spec.: 9 sinistral ♂, 9 dextral ♂, 26 ♀, 2 juv.; 9 cleared and stained), Lake Mainit, Mindanao (type locality, no type status).

This is the only known material of *N. thessa*. Aurich (1937) indicated that he based his original description on at least one male (26 mm SL) and one female (29 mm SL), without giving place of deposition of any type or other material. No specimens of *Neostethus thessa* are present in collections of the ZMB (H. J. Paepke, pers. comm.) and ZMH (H. Wilkens, pers. comm.). However, I do not designate a neotype from the CAS-SU material, even though it is from the type locality, because Aurich's material may eventually be located upon a thorough search of possible collections, and, to my knowledge, there has never been confusion or concern among ichthyologists over identification of the species associated with the name *Solenophallus thessa* Aurich.

DISTRIBUTION.—Lake Mainit, Mindanao, Philippines (Fig. 1).

Neostethus ctenophorus (Aurich, 1937),
new combination
(Fig. 1)

Solenophallus ctenophorus Aurich, 1937:272–275, table 1, figs. 6, 7II–V (original description, Laguna de Bay, Luzon, Philippines).

Ctenophallus ctenophorus (Aurich). Herre 1939:144 (referral

to new genus); 1942:154–155 (characters, distribution, relationships); 1953:240 (synonymy).

REMARKS.—Herre (1942:154) diagnosed *Ctenophallus* as distinct “. . . from other phallostethids by the presence of a dense fringe along both margins of the open groove on the priapium.” This statement was extracted from Aurich's (1937) original description based on at least one male (24 mm SL) and one female (20 mm SL). Place of deposition of type or other material was not given by Aurich. No specimens of *N. ctenophorus* are present in collections of the ZMB (H. J. Paepke, pers. comm.) or the ZMH (H. Wilkens, pers. comm.).

The “dense fringe” is formed by the numerous bony projections of the papillary bone, diagnostic of *Neostethus*. The same character was also used by Myers (1935) to diagnose his new genus, *Plectrostethus*, literally a “quill on the chest,” placed here in synonymy of *Neostethus*.

I have examined no specimens of *N. ctenophorus*; however, without this species, the genus *Neostethus* is paraphyletic. Therefore, I synonymize *Ctenophallus* with *Neostethus*. Meristic data summarized in Table 2 are from Aurich (1937).

DISTRIBUTION.—Laguna de Bay, Luzon, Philippines.

Neostethus robertsi new species

(Figs. 1, 12, 13)

HOLOTYPE.—CAS 50723, dextral ♂, 22.3 mm SL, Calasiao R., about 12 km N of San Carlos City, Pangasinan Prov., Luzon, Philippines, 16 Mar. 1976, T. R. Roberts, coll.

PARATYPES.—CAS 64254 (40 spec.: 12 sinistral ♂, 9 dextral ♂, 10 ♀, 9 juv. or sex undet., 9.0–23.0 mm SL; 1 sinistral ♂, 1 dextral ♂ and 1 ♀ cleared and stained), collected with holotype.

DIFFERENTIAL DIAGNOSIS.—*Neostethus robertsi*, like *N. palawanensis*, has a second ctenactinium which is bifurcated distally, but distinguished from that species by having a larger, better-developed, claw-shaped second ctenactinium, and a slightly bowed second ctenactinium that lacks a fleshy, ventral ridge.

DESCRIPTION.—A small, laterally compressed species, largest size recorded 23.0 mm SL. No vestigial pelvic fin rays or bones in adult females; males with pelvic and parts of pectoral fin modified into priapium that is either dextral (holotype and eight ♂ paratypes) or sinistral (13 ♂ paratypes). Prominent externalized subcephalic bone a first ctenactinium, arising on either left or right



FIGURE 12. *Neostethus robertsi* new species. Holotype (CAS 50723), dextral male, 22.3 mm SL.

side of body and articulating with posterior extent of left or right (proctal) axial bone, curving gently along the left or right side of the head and the tip lying just ventral to lower jaw. First ctenactinium smooth, without fleshy, ventral ridge. Large, well-developed, claw-shaped second ctenactinium. Fibrous pulvinulus lateral to, and covering articulation point of, inner pulvinular and proctal axial bones. Pleural ribs of fourth vertebra in males expanded anteroposteriorly, their distal tips meeting on right side of proctal axial bone in sinistral males and left side in dextral males. First pleural rib on third vertebra in females.

Ventral dermal keel extending from posterior extent of priapium in males or urogenital opening in females, to anal fin origin. Scales on body of moderate size, deciduous. Color in alcohol like most other phallostethids: ground coloration very pale yellow or light brownish (straw-colored). Dark brown melanophores scattered on dorsal surface of head, along midlateral intermuscular septum, on operculum and priapium, and along basal portion of anal fin, dorsal and ventral midline. Dorsal scales with faint dark margins. Eyelens large.

Skull and jaws like those illustrated for *Neostethus bicornis* by Roberts (1971b), with little modification. Jaw teeth small, conical, in a single uneven row or grouped together in indistinct rows.

Caudal skeleton with two epurals, autogenous parhypural, and a dorsal and a ventral hypural plate. Caudal fin rays broken in nearly all specimens examined. Pectoral fin narrow and elongate, with 10–11 rays. Two dorsal fins, the first with two spines or thickened rays supported by a single pterygiophore, the second with 6 rays. Anal fin rays 17–18, vertebrae 36, scales in a

lateral series 30, branchiostegal rays 5 (see Table 2).

DISTRIBUTION.—Pangasinan Prov., Luzon, Philippines (Fig. 1).

ETYMOLOGY.—The specific name, *robertsi*, in honor of Tyson R. Roberts, collector of the type series and student of phallostethid fishes.

Subfamily Gulaphallinae Aurich Tribe Gulaphallini new status

DIAGNOSIS.—Adult males with a perforated gular flap of skin through which anterior end of first ctenactinium projects and remains while at rest; and an aproctal axial bone that projects beyond ventral body profile with a small postero-dorsal crest.

Genus *Gulaphallus* Herre, 1925

Gulaphallus Herre, 1925:508 (type species: *Gulaphallus eximius* Herre, 1925, by subsequent designation of Myers 1928: 9).

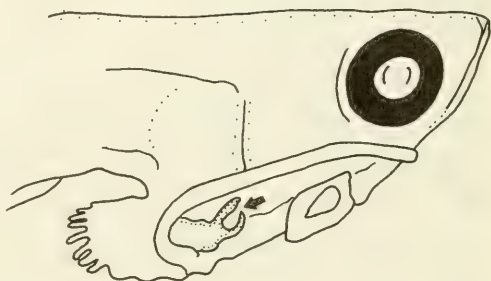


FIGURE 13. Diagrammatic representation of head and anterior portion of body, *Neostethus robertsi*, dextral male, CAS 50723. Anterior to the right. Arrow points to second ctenactinium.

Mirophallus Herre, 1926:539 (type species: *Mirophallus bikolanus* Herre, 1926, by monotypy).

Acanthostethus Herre, 1929:141–142 (type species: *Gulaphallus falcifer* Manacop, 1936, by original designation; preoccupied by *Acanthostethus* Smith, 1869 in Hymenoptera).

Manacopus Herre, 1940a:141 (replacement name for *Acanthostethus* Herre, 1939, and therefore taking same type species: *Gulaphallus falcifer* Manacop, 1936).

DIAGNOSIS.—As for the tribe *Gulaphallini*, above.

COMPOSITION AND DISTRIBUTION.—Five species, four from freshwater hill-streams, Luzon, *G. eximius* Herre, 1925, *G. mirabilis* Herre, 1925, *G. falcifer* Manacop, 1936, and *G. bikolanus* (Herre, 1926), and one from coastal brackish to marine localities, Panay, *G. panayensis* (Herre, 1942), Philippines.

Gulaphallus eximius Herre, 1925

(Fig. 1)

Gulaphallus eximius Herre, 1925:509–510, pls. 1, 2; figs. 1, 2 (original description, Nueva Vizcaya Province, Luzon, Philippines). Myers 1928:9 (characters). Herre 1939:142 (characters, distribution). Hubbs 1944:73 (characters). Herre 1953:241 (distribution).

DIFFERENTIAL DIAGNOSIS.—*Gulaphallus eximius*, the largest phallostethid species, reaches 37 mm SL, and has more than 50 (range 52–58) scales in lateral series, as opposed to 25–38, in all other phallostethids. A brown blotch surrounds anus and urogenital openings in immature females. Rudimentary pelvic girdle represented by two small scale-shaped discs of bone in adult females. Males dextral as in *G. bikolanus*, but unlike that species, a first dorsal fin is present in both sexes.

MATERIAL.—Lectotype (designated by Böhlke 1953): CAS-SU 24474, ♂ 33.5 mm SL, creek, Santa Fe, Nueva Vizcaya Prov., Luzon, Philippines, 18 May 1924, R. C. McGregor, coll. Paralectotypes: CAS-SU 18149 (3 spec.: 1 ♂, 2 ♀), collected with lectotype.

OTHER MATERIAL.—PHILIPPINES: BMNH 1933.3.11.168 (1 ♂, 32.2 mm SL), FMNH 40593–40596 (4 spec.: 1 ♂, 2 ♀, 1 immature ♂), CAS-SU 38900 (72 spec.; 11 cleared and stained), CAS-SU 36832 (4 spec.: 1 ♂, 2 ♀, 1 juv.), Luzon.

DISTRIBUTION.—Mountain streams, Luzon, Philippines.

Gulaphallus mirabilis Herre, 1925

(Figs. 1, 4, 5)

Gulaphallus mirabilis Herre, 1925:511, pl. 2, figs. 3–5 (original description, Ibo creek, tributary of Angat R., Bulacan Province, Luzon, Philippines). Myers 1928:10 (characters). Villaladilid and Manacop 1935:196–217, pls. 1–4, figs. 1–3 (anat-

omy, development). Bailey 1936:457–470, pls. 1, 2 (osteology). Aurich 1937:275–279, figs. 8, 9 (anatomy). Myers 1937:142 (characters). TeWinkel 1939:63–67 (anatomy, development). Herre 1939:142 (characters, distribution); 1942:144–145 (characters, distribution, relationships). Hubbs 1944:73 (characters). Herre 1953:241 (distribution). Roberts 1971b:411 (characters). Grier et al. 1980:332, table 1 (testis structure). Rosen and Parenti 1981:20, fig. 19B (dorsal gill arch anatomy).

DIFFERENTIAL DIAGNOSIS.—*Gulaphallus mirabilis* is readily distinguished from congeners by scales in lateral series ranging from 36 to 38 as opposed to from 28 to 32, or more than 50.

MATERIAL.—PHILIPPINES: Luzon: ANSP 91045 (4 spec.: dextral ♂, ♀, 2 juv., 12–25 mm SL), BMNH 1933.3.11.169–186 (18 spec.: 3 dextral ♂, 2 sinistral ♂, 11 ♀, 2 immature; 1 dextral ♂ and 1 ♀ cleared and stained), FMNH 76769 (6 spec.: 1 dextral ♂, 5 juv.), CAS 727 (1), CAS 728 (1), CAS 731–735 (5), CAS 740–743 (4), CAS 747–751 (5), CAS-SU 30720 (165), CAS-SU 38903 (64 spec.; 5 cleared and stained), CAS-SU 35959 (25), CAS 54938 (2 spec.: 1 sinistral ♂, 1 ♀), CAS-SU 35958 (121 spec.: 11 sinistral ♂, 15 dextral ♂, 32 ♀, 63 juv.), FMNH 46946 (9 spec.: dextral ♂, 4 ♀, 4 juv.), USNM 94293 (26 spec.: 8 dextral ♂, 4 ♀, 14 juv.), USNM 104412 (2), MCZ 33904 (10), MNHN 27-192, 193 (25, labelled syntypes, but not from type locality), MNHN 32-204 (4), ZMA 100.651 (4 spec.: 1 dextral ♂, 1 ♀, 2 juv., 17–29 mm SL), Molawin Creek, CAS-SU 38209 (7), CAS 50721 (279), UMMZ 211664 (54), Olo Creek, CAS-SU 38901 (7), CAS-SU 38902 (1 cleared and stained), Sison, and CAS 50719 (230), Barabac Creek, Pangasinan Prov.; CAS-SU 38904 (43 spec.: 4 sinistral ♂, 6 dextral ♂, 24 ♀, 9 juv., 13–31 mm SL; 2 dextral ♂ and 2 ♀ cleared and stained), FMNH 40623–40627 (4 spec.: 2 sinistral ♂, 2 ♀), Santa Maria R.; MCZ 33904 (10), Los Banos, Laguna Prov.; USNM 197728 (31 juv.), Central Luzon; CAS 50720 (23 spec.: 3 sinistral ♂, 2 dextral ♂, 8 ♀, 10 juv.), Porac R., Pampanga Prov.

DISTRIBUTION AND REMARKS.—One of the best-known and frequently collected phallostethid species because of its abundance in Molawin Creek, which flowed through the campus of the College of Agriculture, Luzon, Philippines (Herre 1942). Known also from other localities throughout Luzon.

Gulaphallus falcifer Manacop, 1936

(Fig. 1)

Gulaphallus falcifer Manacop, 1936:375–379, pls. 1, 2 (original description, Barrio Laput, Mexico, Pampanga Prov., and Nampicuan, Nueva Ecija, Luzon, Philippines).

Acanthostethus falcifer (Manacop). Herre 1939:141–143 (referral to new genus).

Manacopus falcifer (Manacop). Herre 1940a:141 (referral to new genus); 1942:146–147 (characters, distribution, relationships); 1953:241 (synonymy). Parenti 1986b:306–309, figs. 1–3 (anatomy, development).

DIFFERENTIAL DIAGNOSIS.—*Gulaphallus falcifer* is the only phallostethid species in which

females as well as males exhibit bilateral asymmetry: adult females with an elongate pelvic fin ray, on either left or right pelvic girdle, that projects beyond body profile to left or right of urogenital openings.

MATERIAL.—PHILIPPINES: Luzon: CAS-SU 32356 (42 spec.: 9 sinistral ♂, 14 dextral ♂, 10 sinistral ♀, 3 dextral ♀, 6 juv.; 7 cleared and stained), Barrio Laput, Pampanga Prov. (type locality). No locality: CAS 63198 (2 cleared and stained).

REMARKS.—Manacop (1936) lists the following type material: Holotype: Philippine Fish and Game Administration 31778, adult ♂, 27.5 mm SL, gourami pond at Barrio Laput, Mexico, Pampanga Prov., Luzon, Philippines, 27 Aug. 1935, C. Sandiko, coll. Allotype (=paratype): Philippine Fish and Game Administration 31779 (adult ♀ 26.5 mm SL). Paratypes: Philippine Fish and Game Administration 31780 (17 spec.: 8 ♀ and 9 ♂). This material is presumed unavailable for study. Böhlke (1953) did not designate a neotype from the CAS-SU material.

DISTRIBUTION.—Barrio Laput, Pampanga Prov., Luzon, Philippines.

Gulaphallus bikolanus (Herre, 1926),
new combination
(Fig. 1)

Mirophallus bikolanus Herre, 1926:540–541, pl. 3 (original description, Lake Bato, Camarines Sur Province, and Lake Lanigay, Albay Province, Luzon, Philippines). Myers 1928: 10–11 (characters). Aurich 1937:279–282, fig. 10 (anatomy). Myers 1937:142 (characters). Herre 1939:142 (distribution); 1942:142 (characters, distribution, relationships). Hubbs 1944:73–74 (characters). Herre 1953:241 (distribution). Parenti 1986a:234, table 2 (bilateral asymmetry).

DIFFERENTIAL DIAGNOSIS.—Males of *Gulaphallus bikolanus* are dextral as in *G. eximius*, but unlike that species, both males and females of *G. bikolanus* lack a first dorsal fin and have 32 scales in a lateral series, as opposed to more than 50.

MATERIAL AND REMARKS.—Lectotype (designated by Böhlke 1953). CAS-SU 24475, immature ♂, 19.5 mm SL, Lake Bato, Camarines Sur Prov., Luzon, Philippines, 30 Jan. 1926, G. A. Lopez, coll. Paralectotypes: CAS-SU 18148 (2 ♀, 22–23 mm SL), MNHN 27-194 (2, 21.1–23.8 mm SL), collected with lectotype. Böhlke (1953) was apparently unaware of the MNHN specimens, collected with the syntypes, which also have paralectotype status.

OTHER MATERIAL.—PHILIPPINES: AMNH 50592 (24 spec.: 13 dextral ♂, 9 ♀, 2 juv.), CAS 50722 (194 spec.: 131 dextral ♂, 55 ♀, 8 juv.), Guinobatan R., CAS 53165 (70 spec.: 24 dextral ♂, 37 ♀, 9 juv.), UMMZ 211665 (12 spec.: 5 dextral ♂, 7 ♀), Cabangan R., Albay Prov., Bikol Region, Luzon.

DISTRIBUTION.—Camarines Sur and Albay provinces, Luzon, Philippines.

Gulaphallus panayensis (Herre, 1942),
new combination
(Fig. 1)

Neostethus (Sandakanus) panayensis Herre, 1942:153 (original description, Capiz and Estancia, Panay, Philippines); 1953: 242 (distribution).

DIFFERENTIAL DIAGNOSIS.—*Gulaphallus panayensis* is a small, slender species known only from limited type material, with vertebrae 31–33, as opposed to 35–37, and scales in lateral series 28–30, as opposed to 32–58 in congeners. The largest male (holotype) does not have a completely developed priapium; however, I conclude, primarily from examination of cleared and stained specimens, that *panayensis* is a *Gulaphallus*.

MATERIAL.—Holotype: CAS-SU 36539, dextral ♂, 19.0 mm SL, Capiz, Panay, Philippines, 3 Aug. 1940, A. W. C. T. Herre, coll. Paratypes: CAS-SU 36540 (22 spec.: 1 sinistral ♂, 3 dextral ♂, 18 ♀; 2 cleared and stained) collected with holotype, and CAS-SU 36541 (22 spec.: 5 dextral ♂, 15 ♀, 2 juv.), Estancia, Panay, Philippines, 27 July 1940, A. W. C. T. Herre, coll.

DISTRIBUTION.—Capiz and Estancia, Panay, Philippines (Fig. 1).

CONCLUSIONS

1. The Phallostethidae comprise a monophyletic group of 19 species, classified in four genera, of three monophyletic tribes—Phallostethini, Neostethini, and Gulaphallini. Phallostethini (containing *Phallostethus* and *Phenacostethus*) and Neostethini (containing solely *Neostethus*) are sister taxa comprising the subfamily Phallostethinae. Subfamily Gulaphallinae is coextensive with tribe Gulaphallini and genus *Gulaphallus*.

2. Of the 19 recognized species, one, *Neostethus robertsi*, from Luzon, Philippines, is described as new. *Neostethus siamensis* Myers, 1937 is placed in synonymy of *Neostethus lankesteri* Regan, 1916; *Neostethus coronensis* Herre, 1942 is placed in synonymy of *Neostethus borneensis* Herre, 1939. Five new combinations are proposed: *Plectrostethus palawanensis* Myers, 1935, *Solenophallus thessa* Aurich, 1937 and *S. ctenophorus* Aurich, 1937, are placed in *Neostethus*; *Mirophallus bikolanus* Herre, 1926 and *Neoste-*

thus *panayensis* Herre, 1942 are placed in *Gulaphallus*.

3. All known names proposed for parts of the bilaterally asymmetric priapium are listed and defined; synonyms and presumed homologs are identified. Derived characters of the priapium provide the primary information for species group recognition. However, bilateral asymmetry in females of one species (*G. falcifer*), elaborate urogenital coverings in females of three species (*N. lankesteri*, *N. borneensis*, and *N. villadolidi*), and ontogenetic changes in pigmentation pattern of the anus and urogenital openings in females of one species (*Gulaphallus eximius*) indicate that the complex evolution of the male priapium has been paralleled by numerous modifications in the reproductive system of females.

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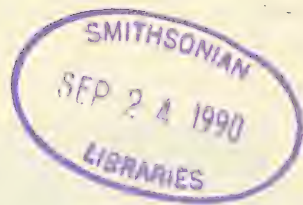
Comments of several reviewers greatly improved the presentation of ideas.

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NEW AND RECONSIDERED MEXICAN ACANTHACEAE. IV.

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ABSTRACT: *Dyschoriste mcvaughii*, characterized by its diminutive habit, red corollas, and inconspicuously spurred thecae, is newly described from western Jalisco. The monotypic genera *Ixtlania* and *Tabascina* are considered to be congeneric with *Justicia* and the new names, *J. ixtlania* and *J. tabascina* are provided. A new combination, *Schaueria parviflora*, is proposed for the species resulting from the taxonomic merger of *Streblacanthus parviflorus* and *Schaueria calycobractea*.

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INTRODUCTION

Ongoing studies of the more than 350 species of Acanthaceae in Mexico continue to necessitate the description of new and the reevaluation of previously described taxa. In this report, a remarkable red-flowered species of *Dyschoriste* is described for the first time. Recent collections and studies of two monotypic genera, *Ixtlania* M. E. Jones and *Tabascina* Baillon, reveal them to be congeneric with the large and polymorphic genus *Justicia* L. *Schaueria calycobractea* R. Hilsenbeck & D. Marshall, a species recently described from Veracruz, is shown to be correctly classified generically but conspecific with the previously described *Streblacanthus parviflorus* Leonard from Guatemala and thus in need of nomenclatural renovation. Detailed descriptions are provided for each of these taxa.

Dyschoriste mcvaughii T. F. Daniel, sp. nov.

(Figures 1, 2f)

TYPE.—MEXICO, Jalisco: between Ayutla and Mascota near summit of pass, 7–8 mi NW of Los Volcanes, 30 April 1951, R. McVaugh 12187 (Holotype: MICH!; isotype: US!).

Herba perennis usque ad 1 dm alta. Folia sessilia vel subsessilia petiolo usque ad 2 mm longo, elliptica vel obovata, 4–18 mm longa, 3–7 mm lata, 1.1–4-plo longiora quam latiora. Dichasia 1–3-flora, in axillis foliorum distalium sessilia vel subsessilia. Bracteolae et bracteolae secundae lineares vel lineares-ellipticae vel lineares-oblancoolatae, 5.5–11 mm longae, 1–3 mm latae. Calyx 9–12 mm longus lobis tubo 1.4–3-plo longioribus. Corolla rubra, 34–42 mm longa. Stamina 9–14 mm longa, thecae 1.8–2.4 mm longae, basi inconspicuae calcaratae vel muticae. Stylus 27–38 mm longus. Capsula 7 mm longa, glabra.

Perennial herb from woody rhizome to 1 dm tall, with numerous woody roots. Stems subquadrate to quadrate-sulcate, densely pubescent with straight to flexuose eglandular trichomes 0.1–0.3(–0.5) mm long. Leaves sessile or subsessile with petioles to 2 mm long, blades elliptic to obovate, 4–18 mm long, 3–7 mm wide, 1.1–4 times longer than wide, rounded to acute at apex, rounded to acute to cuneate at base, surfaces pubescent (especially along veins) like stems (although the trichomes tending to be more antrorse), proximal leaves reduced in size, 1.5–3 mm long. Inflorescence of 1–3-flowered dichasia borne in axils of distal leaves forming a terminal spicate thyrses, dichasia sessile or sub-

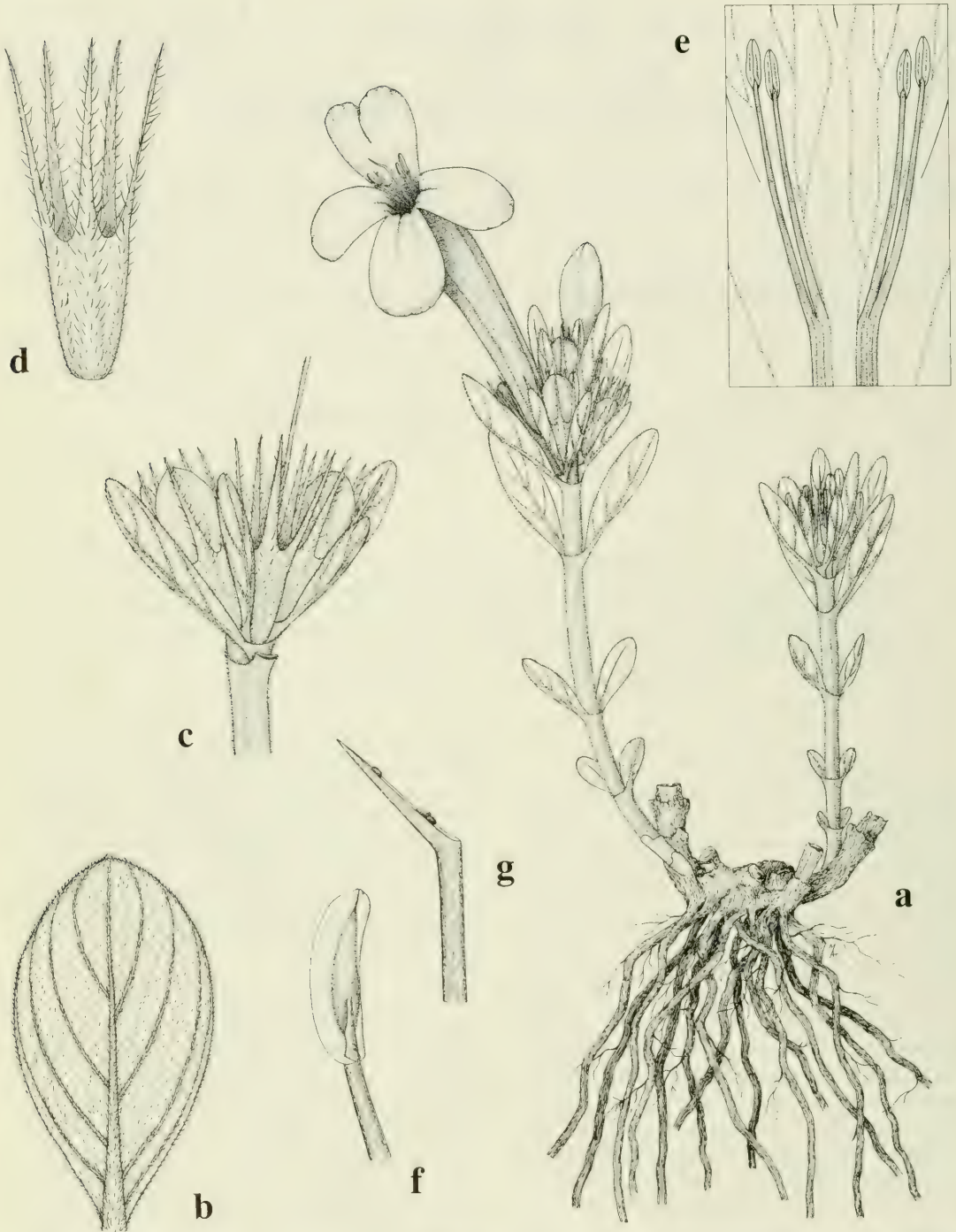


FIGURE 1. *Dyschoriste mcvaughii*. a, habit, $\times 1.2$ (McVaugh 12187); b, leaf, $\times 4$ (Daniel & Bartholomew 4828); c, flowering node with leaf removed showing 3-flowered dichasium, $\times 3$ (McVaugh 12187); d, calyx, $\times 5$ (McVaugh 12187); e, androecium in opened corolla, $\times 5$ (Daniel & Bartholomew 4828); f, distal portion of stamen, $\times 12$ (McVaugh 12187); g, distal portion of style and stigma, $\times 15$ (Daniel & Bartholomew 4828).

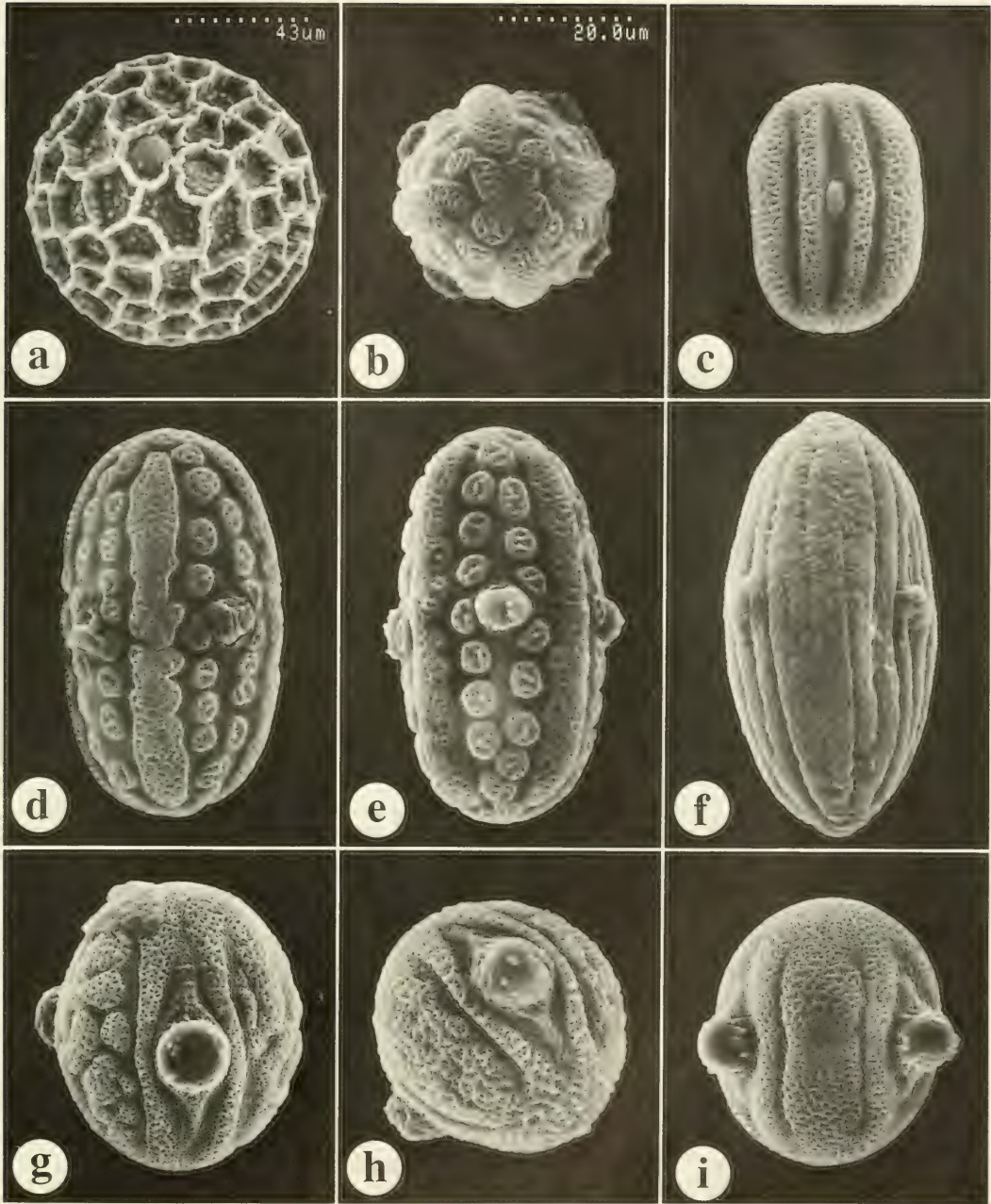


FIGURE 2. Scanning electron micrographs of pollen. a, *Ruellia petiolaris* (Nees) T. Daniel (Daniel & Breedlove 4930); b, *Justicia tabascina* (Cowan 2860), polar view; c, *Justicia ixtlania* (Daniel 2070), equatorial view; d, *J. tabascina* (Cowan 2860), equatorial view showing surface between 2 trema regions; e, *J. tabascina* (Cowan 2860), equatorial view showing 1 trema region; f, *Dyschoriste mcvaughii* (Daniel 4828), equatorial view; g, *Schaueria parviflora* (Trigos 198), equatorial view; h, *S. parviflora* (Herrera 72), subequatorial view; i, *S. parviflora* (Contreras 11180), equatorial view. Scale in c-i same as in b.

sessile with peduncles to 1.5 mm long. Bractlets and secondary bractlets linear to linear-elliptic to linear-oblongate, 5.5–11 mm long, 1–3 mm wide, pubescent like leaves. Calyx 9–12 mm long, tube 3–5 mm long, hyaline between veins, lobes subulate, 6–9 mm long, 1.4–3 times longer than tube, aristate and becoming stiff apically, pubescent like leaves. Corolla red, 34–42 mm long, externally pubescent with flexuose eglandular trichomes, tube 24–33 mm long, slightly curved and gradually ampliate distally but not differentiated into a well-defined throat, upper lip 9–11 mm long with 2 subcirculate lobes 4.5–6 mm long, 4.5–7 mm wide, lower lip 8.5–12 mm long with 3 lobes obovate-elliptic to obovate, 8–10 mm long, 5–7 mm wide. Stamens didynamous, 9–14 mm long, the two pairs fused for 1–2 mm at base, thecae 1.8–2.4 mm long, mucous or with blunt to pointed appendages 0.05–0.1 mm long at base, pollen prolate, 3-colporate, intercolpal regions multi-striate with 5–14 pseudocolpi of irregular lengths, exine minutely verrucate. Style 27–38 mm long, pubescent with eglandular trichomes, stigma filiform, 1.3–1.5 mm long. Capsule ellipsoid, 7 mm long, glabrous. Seeds not seen.

DISTRIBUTION AND HABITAT.—Central and western Jalisco (Fig. 3); in disturbed areas of oak and oak-pine forest at elevations from 1,600 to 1,900 m.

PHENOLOGY.—Flowering: March–June.

Emery Leonard annotated McVaugh's collection as an undescribed species of *Ruellia* L. On the basis of many of its macromorphological attributes, this species might indeed be mistaken for *Ruellia*. *Dyschoriste* Nees is usually easily distinguished from *Ruellia* by the presence of conspicuous pointed appendages at the base of each theca which are not known among American *Ruellia*. In *D. mcvaughii* these appendages are inconspicuous or absent. Characters of the pollen and calyx preclude the placement of this species in *Ruellia*, however. Pollen of *Ruellia* (Fig. 2a) is spherical and three-porate (Raj 1961, 1973). It is best characterized by its homobrochate-reticulate exine. Pollen of *Dyschoriste* (Fig. 2f) is prolate and three-colporate. The exine is verrucate with minute, rounded projections and striate with multiple pseudocolpi between the colpi. In Mexican *Dyschoriste*, the calyx tube is often prominently angled and hyaline between the major veins which extend into the lobes. The

tube commonly ruptures at maturity in these weak regions. In most species of *Dyschoriste*, the calyx lobes are long attenuate to aristate and become stiff at maturity. Although there is considerable variation in calyx form among Mexican species of *Ruellia*, none have a partially hyaline tube with stiff, aristate lobes. In features of both pollen and calyx form, the plants described here conform to other species of *Dyschoriste*.

The reduced thecal appendages of *D. mcvaughii* are an unusual feature in the genus. Anthers of McVaugh 12187 vary from having blunt appendages to lacking appendages altogether. Daniel and Bartholomew 4828, collected in the same general region, has anthers with the pointed appendages typical of other species of *Dyschoriste*. Elsewhere in the genus, variation of thecal appendages is evident among the Chiapas collections of *D. ovata* (Cav.) Kuntze cited by Daniel (1986). In these collections, thecal appendages vary from one or more hairlike projections to a single stout mucro.

Kobuski (1928) revised the American species of *Dyschoriste* and recognized 21 species as occurring in Mexico, none of which are similar to *D. mcvaughii*. Among the 40 American species he treated, only *D. pringlei* Greenman from Jalisco has corollas similar in size to those of *D. mcvaughii*. Recent study of *D. pringlei* for McVaugh's *Flora Novo-Galiciana* (Daniel, unpublished) reveals that this species differs from *D. mcvaughii* by having conspicuously flattened young stems, the dichasia crowded at or near the stem apex resulting in a headlike floral cluster, and blue corollas. A closer relative is undoubtedly *D. rubiginosa* Ramamoorthy & Wassh., a species with large reddish corollas recently transferred to *Dyschoriste* from *Hygrophila* R. Br. (Ramamoorthy and Wasshausen 1985). These two species can be distinguished from all other Mexican *Dyschoriste* by their reddish corollas and they can be distinguished from one another by the following couplet:

Diminutive perennial herb to 1 dm tall; distal leaves 1.1–4 times longer than wide; flowers 1–3 in leaf axils; bractlets straight; corolla 34–42 mm long; thecal appendages absent or up to 0.1 mm long *D. mcvaughii*
 Perennial herb or shrub to 1.5 m tall; distal leaves 5–15 times longer than wide; flowers more than 3 (up to 16) in leaf axils; bractlets

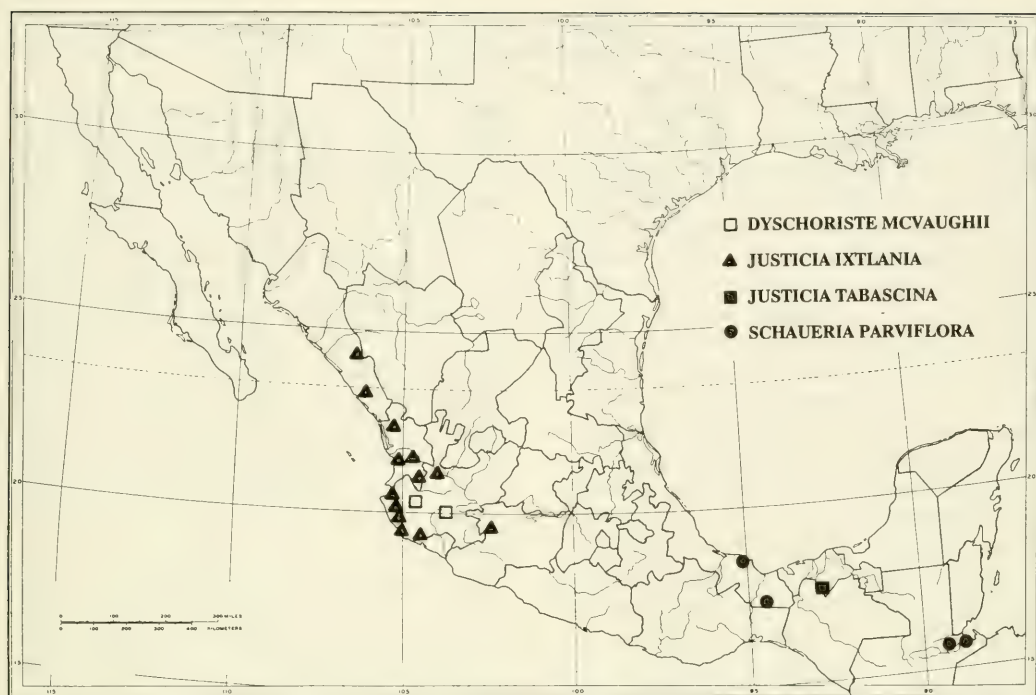


FIGURE 3. Map showing distribution of *Dyschoriste mcvaughii*, *Justicia ixtlania*, *J. tabascina*, and *Schaueria parviflora*.

usually conspicuously curved; corolla (20–) 25–34 mm long; thecal appendages 0.1–0.2 mm long *D. rubiginosa*

PARATYPES.—MEXICO. Jalisco: between Ameca and Aten-
guillo, 14.6–16.2 mi W of Mixtlán, *T. Daniel & B. Bartholomew*
4828 (CAS); Chiquilistlán, *M. Jones* 378 (POM, US); La Pal-
ma, *M. Jones* s.n. (POM).

***Justicia ixtlania* T. F. Daniel, nom. nov.**

Ixtlania acicularis M. E. Jones, Contr. West. Bot. 15:151. 1929.

TYPE.—MEXICO. Nayarit: Ixtlán [del Río], 19 February
1927, *M. E. Jones* 23534 (Holotype: POM!, photo and frag-
ments: US!; isotype: MO!). Not *J. acicularis* Sw. (1788).

Erect to reclined perennial herb to 3 dm tall. Stems subterete to subquadrate, sulcate, pubescent with flexuose to recurved eglandular trichomes 0.5–1.5 mm long, the trichomes evenly disposed or usually concentrated in 2 vertical lines, mature stems often glabrate. Leaves short-petiolate with petioles 2–11 mm long, blades somewhat coriaceous, lanceolate to ovate to elliptic (sometimes narrowly so) to subcirculate to obovate, 12–85 mm long, 11–47 mm wide, 1.1–5 times longer than wide, rounded to acute at

apex, acute to rounded to truncate to subcordate at base, surfaces glabrous or pubescent, margin entire to subcrenate, white-callose. Inflorescence of axillary and/or terminal, densely bracteate, often clustered spikes (or spikelike thyrses) to 5 cm long, rachis pubescent with an understory of straight glandular and eglandular trichomes to 0.1 mm long and an overstory of longer flexuose eglandular trichomes, flowers 1 per node. Bracts sometimes conduplicate, ovate-lanceolate to lance-subulate, (3–)5–10 mm long, 0.8–1.5 mm wide, abaxial surface pubescent with an understory of straight glandular and eglandular trichomes to 0.1 mm long and an overstory of flexuose eglandular trichomes 0.2–1 mm long, margin subscarios and ciliate. Bractlets lanceolate to lance-subulate, (4–)5.5–9 mm long, 0.8–1.5 mm wide, pubescent like bracts. Calyx 5-lobed, 6.5–9 mm long, lobes divided nearly to base, lanceolate to lance-subulate, pubescent like bracts, margins scarios, posterior lobe reduced in size. Corolla entirely white to pink-purplish with purple markings on lower lip, 12–16 mm long, externally pubescent with straight to flexuose eglandular trichomes to 0.6 mm long, tube 8–11 mm

long, slightly ampliate distally, upper lip 3–4 mm long, bilobed with rounded lobes 0.1–0.5 mm long at apex, lower lip 3.5–5 mm long, with 3 subcirculate to obovate lobes 3–4 mm long, 2.5–3.5 mm wide, central lobe larger than lateral lobes. Stamens 3.5–4 mm long, thecae 0.6–1 mm long, unequally inserted, the lower (sometimes slightly larger) with a blunt calcarate basal appendage 0.2–0.3 mm long, pollen prolate, 2-colporate with each colpus flanked by 2 pseudocolpi, exine reticulate. Style 9–11 mm long, glabrous, stigma unlobed, subcirculate, oblique, 0.2–0.3 mm long. Capsule short-stipitate, 3–5 mm long, stipe 0.5–1.3 mm long, head ellipsoid, 2.5–3.7 mm long, externally pubescent with downward pointing to appressed eglandular trichomes 0.2–0.3 mm long and straight glandular trichomes up to 0.1 mm long (mostly near apex). Seeds 4 per capsule, somewhat flattened, subcordate to subcirculate to elliptic in outline, 1–1.3 mm long, 0.8–1.1 mm wide, surface papillose ($n = 14$, *Daniel and Bartholomew 4788*).

DISTRIBUTION AND HABITAT.—West-central Mexico (Sinaloa, Nayarit, Jalisco, and Michoacán) (Fig. 3); along streambanks in deciduous or subdeciduous forest at elevations from 150 to 1,250 m.

PHENOLOGY.—Flowering and fruiting: March–April.

Leonard (1945) accepted *Ixtlania* as a viable genus, considered a probable relationship with *Beloperone* Nees, and noted a superficial resemblance to *Chaetothylax* (erroneously cited as “*Chaetochlamys*”) *umbrosus* Nees of South America. *Chaetothylax* Nees differs from *Ixtlania* by having four (vs. five) calyx lobes, dimorphic thecae with the lower theca reduced or appearing abortive and separated from the upper theca by about 1 mm (vs. homomorphic thecae that are in contact with one another), and pubescent (vs. glabrous) seeds.

In a recent delimitation and infrageneric classification of *Justicia*, Graham (1988) included both *Beloperone* and *Chaetothylax* within *Justicia*. She did not examine material or discuss the disposition of *Ixtlania*, however. On the basis of the diagnostic characters of the corolla (i.e., regulate) and androecium (i.e., two stamens with bithecaous anthers, the lower thecae with basal appendages), it is clear that *Ixtlania* is likewise congeneric with the large and polymorphic *Jus-*

ticia. The chromosome number noted above for this species is also the most common number in *Justicia* (Daniel et al. 1984, in press).

Using Graham's (1988) provisional key to infrageneric taxa of *Justicia*, *J. ixtlania* appears to be most closely affiliated with sect. *Leucoloma* V. Graham from South America. *Justicia ixtlania* differs from the two species of this section by the appendages of the lower thecae which are more than one-fifth of the length of the thecae. It resembles Graham's description of this section in most other aspects, however, including the pollen form (Fig. 2c). In *Justicia* two-colporate, four-pseudocolpate pollen is known only in sect. *leucoloma* and two sections restricted to the Old World. This type of pollen has also been reported in *Mexacanthus* T. Daniel (Daniel 1981), a monotypic genus of Odontoneminae endemic to Mexico.

Considerable variation in corolla color was noted within living populations of this species. The specimen from Michoacán differs from those from Jalisco, Nayarit, and Sinaloa by its narrower, lanceolate to narrowly elliptic to oblanceolate leaves. In other respects it is identical to the more northerly collections.

ADDITIONAL SPECIMENS EXAMINED.—MEXICO. Jalisco: vic. of Arroyo de Chorillo (tributary of Río de Quimixto), ca. 14 km SW of Puerto Vallarta, *A. Carter & F. Chisaki 1249* (MEXU, MICH, UC); Mpio. Cuautitlán, 1.5–2 km W de Tequesquiltán, *R. Cuevas G. 1052* (CAS); along Hwy. 200 S of Puerto Vallarta, 7.6 mi S of El Tuito, *T. Daniel 2070* (ASU, CAS, DUKE, K, MEXU, MO); between Tomatlán and Talpa de Allende, ca. 11 mi N of Tomatlán, *T. Daniel 2086* (ASU); along Hwy. 15 ca. 1 mi E of Nayarit border, *T. Daniel & B. Bartholomew 4788* (CAS); Mpio. La Huerta, Est. Biol. Chamela, Arroyo Chamela, *E. Lott 967* (ASU, CAS, DUKE, MO); Mpio. Tequila, Barranca de los Tanques, desv. al camino de San Martín de las Cañas, *L. Puga 6114* (IBUG). Michoacán: Los Chorros del Varal, Los Reyes, *B. Guillén Jiménez s.n.* (IBUG). Nayarit: 30 km NE of Tepic, 2 km E of Poichotitlán, *M. Baker 1104* (ASU); La Bahada, SE of San Blas, *E. Lehto 24208* (ASU); San Felipe to Arroyo San José del Conde, *Y. Mexia 1930* (A, CAS, F, GH, MICH, UC, US); Potrero la Taberna, km 28 de Amatlán de Cañas, carr. Tepic-Barranca del Oro, *B. Ahuet Juan R. s.n.* (IBUG). Sinaloa: along Hwy. 40 between Villa Union and Cd. Durango, 26 mi SW of Tropic of Cancer, *T. Daniel 4019* (CAS); near Microondas tower near Villa Union, *E. Lehto 24273A* (ASU); Mpio. Concordia, along Hwy. 40 ca. 5 mi NE of Concordia, *A. Sanders et al. 4996* (CAS); Mpio. Cosalá, arroyo NE de Guadalupe de Los Reyes, *P. Tenorio L. et al. 8345* (CAS).

***Justicia tabascina* T. F. Daniel, nom. nov.**

Tabascina lindenii Baillon, Hist. Pl. 10:445. 1891. (as *T. lindenii*) TYPE.—MEXICO. Tabasco: forêts de Teapa, October,

J. Linden s.n. (Holotype: Pl, photographs: CAS, F). Not *J. lindenii* Houlet (1870).

Shrub to 2.5 m tall. Young stems subquadrate to quadrate, evenly pubescent with antrorse eglandular trichomes to 0.6 mm long, internodes often constricted just above nodes. Leaves petiolate with petioles to 33 mm long, blades ovate-elliptic to elliptic, 36–165 mm long, 12–83 mm wide, 2–3 times longer than wide, acuminate at apex, acute to subattenuate at base, surfaces pubescent with cauline type trichomes mostly or entirely restricted to major veins. Inflorescence of 1–4 terminal racemose thyse(s) to 7.5 cm long, flowers paired at nodes, sessile to short (to 1 mm) pedicellate in axil of 2 bractlets, the flowers and bractlets pedunculate in axil of a bract with peduncles to 12 mm long, rachis and peduncles evenly pubescent with flexuose to antrorse eglandular trichomes to 0.6 mm long. Bracts often caducous, linear, 4–7 mm long, 0.6–1.5 mm wide, pubescent like rachis. Bractlets linear, 2.5–6 mm long, 0.8–1 mm wide, pubescent like rachis. Calyx 5-lobed, 10–16 mm long, tube 1–2 mm long, lobes valvate or nearly so, anterior lobes often connivent along edges, asymmetrically elliptic to lance-elliptic, 8–11 mm long, 2–3.2 mm wide, posterior lobe ovate-elliptic to elliptic, 10–13 mm long, 4–5 mm wide, all lobes pubescent with straight to flexuose eglandular trichomes to 0.5 mm long. Corolla yellow, 24 mm long, externally pubescent with glandular trichomes 0.05–0.2 mm long, tube 13 mm long, upper lip 11 mm long, entire, internally rugulate, lower lip 10 mm long with 3 rounded lobes to 3 mm long and 2.5 mm wide. Stamens 9 mm long, filaments glabrous, thecae subsagittate, unequally inserted, 5.3 mm long, rounded and lacking basal appendages, pollen prolate, 4-porate (to 4-subcolporate) with pores in a trema region containing 2 longitudinal rows of circular insulae, exine reticulate. Style 15–18 mm long, glabrous, stigma more or less capitate, 0.2 mm long. Capsule 19–22 mm long, glabrous, stipe 8–9 mm long, head 11–13 mm long. Seeds 4, flattened, subcirculate in outline, 4.2–5 mm long, 3.8–4.8 mm wide, the surfaces smooth.

DISTRIBUTION AND HABITAT.—South-central Tabasco (Fig. 3); in lower montane rain forest at an elevation of about 140 m.

PHENOLOGY.—Flowering: March and October; fruiting: March.

The recent rediscovery of plants resembling the type, and only known collection, of *Tabascina lindenii* allows for a reevaluation of this monotypic genus. Cowan's collection was made in the region of the type locality and contains fruits which were unknown to Baillon (1891). Lindau (1895) maintained *Tabascina* as a genus of Justicieae, differing from *Justicia* by its broad, leaflike (vs. narrow) calyx lobes and flowers in terminal cymes (vs. flowers solitary or in spikes or contracted panicles). The rugulate corolla, androecium of two bitheous stamens, and pollen with trema regions studded with circular insulae (Fig. 2d, e) all suggest placement of this species within *Justicia*. The large, foliaceous, and heteromorphic calyx lobes that are nearly or completely valvate constitute an unusual feature of the species; however, among Mexican *Justicia*, *J. caudata* A. Gray also has valvate, or nearly valvate, and partially connivent calyx lobes. The inflorescence of *J. tabascina* consists of a single terminal thyse (i.e., an indeterminate main axis with determinate lateral axes), or a cluster of these. The lateral axes consist of dichasia in which usually only a single peduncled flower develops. Additional floral buds of the dichasia are evident on the youngest portions of the thyse but are represented only by prominent scars on the older portions. In view of the diversity of calyx forms and inflorescence types documented for species of *Justicia*, these characters would not appear to warrant recognition of *Tabascina* as distinct from *Justicia*.

Graham (1988) noted that four-aperturate pollen has been reported in a few New World species of *Justicia* but she was unable to confirm its occurrence. *Justicia tabascina*, with its four-aperturate pollen (Fig. 2b), can not be readily classified in any of the infrageneric taxa recognized by Graham (1988). Pollen of this species differs from Graham's (1988) type 3 pollen, which is characteristic of section *Drejerella* (Lindau) Graham, only by the presence of four rather than three apertures. *Justicia tabascina* exhibits several macromorphological features (e.g., unappendaged thecae) that exclude it from this section, however.

ADDITIONAL SPECIMEN EXAMINED.—MEXICO. Tabasco: Mpio. Tacotalpa, Cerro de Madrigal, 7 km de las Est. Tacotalpa hacia Tapijulapa, C. Cowan et al. 2860 (CAS).

Schaueria parviflora (Leonard) T. F. Daniel, comb. nov.

Streblacanthus parviflorus Leonard, J. Wash. Acad. Sci. 31: 1941. TYPE.—GUATEMALA. Izabal: Escoba, across bay (west) from Puerto Barrios, 3 May 1939, P. Standley 72949 (Holotype: FI).

Schaueria calycobracteata Hilsenbeck & Marshall, Brittonia 35: 362. 1983. TYPE.—MEXICO. Veracruz: Estación de Biología Tropical Los Tuxtlas, 22 July 1978, D. Marshall 1 (Holotype: US fide Hilsenbeck and Marshall 1983 but not located there in 1989; isotypes: MEXU, TEX!, US).

Perennial herb to shrub to 2 m tall. Young stems subquadrate to quadrate-sulcate (often somewhat compressed), sparsely pubescent in 2 decussate lines with antrorse to flexuose to retrorse eglandular trichomes 0.1–0.4 mm long, soon glabrate. Leaves petiolate with petioles to 80 mm long, (lance-ovate to) ovate to ovate-elliptic, 50–180 mm long, 14–90 mm wide, 2–3.6 times longer than wide, acuminate to subfalcate at apex, (subcordate to) rounded to acute and usually somewhat asymmetric at base, surfaces glabrous (or pubescent along midvein of adaxial surface with cauline type trichomes). Inflorescence of terminal, sessile to pedunculate spikes to 55 mm long, peduncles to 15 mm long, rachis pubescent with antrorse to flexuose to retrorse eglandular trichomes 0.1–0.2 mm long either in 2 lines or more or less evenly disposed, flowers opposite in axils of bracts (sometimes in axils of distalmost pair of leaves as well). Bracts linear-lanceolate to lance-subulate, 12–22 mm long, 1.2–2.2 mm wide, abaxial surface glabrous to very sparsely pubescent with antrorse eglandular trichomes 0.1 mm long (especially distally) and rarely with glandular trichomes 0.05–0.1 mm long as well, margin sparsely ciliate with similar trichomes. Bractlets linear-setaceous to lance-subulate, 7–30 mm long, 0.8–1 mm wide, pubescent like bracts although always with glandular trichomes. Calyx 5-lobed, 10–25 mm long, lobes linear-setaceous to subulate, 9–24 mm long, 0.5–1.5 mm wide, irregularly unequal (with 2 or more lobes up to 25% longer and 50% wider than the others), 9–24 times longer than the tube, pubescent like bractlets. Corolla yellow (or white in Guatemala), 22–28 mm long, externally pubescent with eglandular trichomes 0.1–0.2 mm long, tube 14–18.5 mm long, ampliate at base and apex, upper lip 4.5–10 mm long, emarginate with 2 rounded lobes 0.3–0.7 mm long, lower lip 5.5–9.5 mm long with 3 lobes, lateral lobes linear to elliptic to oblanceolate-elliptic, 5–7 mm long,

1.2–2.8 mm wide, central lobe elliptic to oblanceolate, 5.5–7 mm long, 1.5–3 mm wide. Stamens attached 3.5–5 mm proximal to mouth of corolla, 8–9 mm long, thecae parallel, equally inserted, subequal, 1.4–2.5 mm long, pointed at base, pollen subspheric, 3-colporate with each colpus flanked by 2 pseudocolpi, pseudocolpi sometimes fused in intercolpal regions forming a pseudocolpal ring, exine reticulate, reticulum of intercolpal regions sometimes irregularly divided or fragmented. Style 19–23 mm long, glabrous, stigma bilobed with lobes 0.2 mm long. Capsule clavate, 10.5–16 mm long, glabrous (or pubescent with sparse glands to 0.05 mm long in Guatemala), stipe 4.5–8.5 mm long, head 6–9 mm long, retinacula 2–2.8 mm long. Seeds 4, flat, subcirculate to subcordate in outline, 3.5–5.2 mm long, 3–4.9 mm wide, surfaces and margin papillose.

DISTRIBUTION AND HABITAT.—Southeastern Mexico (southern Veracruz) and east-central Guatemala (Izabal) (Fig. 3); in lowland to lower montane rainforest (primary and secondary growth) from near sea level to 700 m.

PHENOLOGY.—Flowering: January, March–April, July, and October; fruiting: March, June–July, and October.

In the protologue of *Streblacanthus parviflorus*, Leonard (1941) noted a relationship with *S. cordatus* Lindau, a species of southern Central America. Gibson (1974) noted the occurrence of four calyx lobes in *Streblacanthus* Kuntze and maintained *S. parviflorus* as the northernmost-occurring species in the genus. In 1983, Hilsenbeck and Marshall described *Schaueria calycobracteata* from Veracruz and noted that it appears similar to *Streblacanthus parviflorus* from Guatemala. They further noted that *Streblacanthus* could be distinguished from *Schaueria* Nees by its four-lobed (vs. five-lobed) calyx and unequally (vs. nearly equally) inserted thecae, but that these generic distinctions had not always been followed. They concluded that these genera are very similar and may not deserve separation. I agree with them that further study of the generic limits of *Schaueria* and *Streblacanthus* is desirable. I also concur with placement of the plants from the vicinity of the Estación de Biología Tropical Los Tuxtlas in *Schaueria* based on the distinctions provided above. However, the type of *Streblacanthus parviflorus* and other collec-

tions from Guatemala likewise have five-lobed calyces and subequally inserted thecae. Therefore, they should also be treated in *Schaueria*.

Since the description of *Schaueria calycobracea* (Hilsenbeck and Marshall 1983), in which two collections were cited, additional collections of this species have been made in the vicinity of San Andrés Tuxtla and in the Uxpanapa region about 150 km to the southeast. The three known collections from Guatemala differ from the Mexican collections by the presence of sparsely distributed glandular trichomes (vs. glabrous in Mexico) on the capsules and white (vs. yellowish in Mexico) corollas. Given the overall similarity in all other characters, these distinctions seem relatively minor.

Pollen of *Schaueria parviflora* from Veracruz (Fig. 2g, h) is similar to that of plants from Guatemala (Fig. 2i) and agrees with a description of the type, *S. calycotricha* (Link & Otto) Nees, from South America (Raj 1961).

ADDITIONAL SPECIMENS EXAMINED.—GUATEMALA. Iza-bal: El Estor, *E. Contreras 11180* (LL); between Escobas and Montana Escobas, across bay from Puerto Barrios, *J. Steyermark 39324* (F). MEXICO. Veracruz: Mpio. San Andrés Tuxtla, cerca de Laguna Escondida, entre Sontecomapan y Montepio, *J. Beaman 5763* (F); Mpio. San Andrés Tuxtla, Estación de Biología Tropical Los Tuxtlas, *J. Calzada 764* (F, US), *A. Gómez-Pompa 4484* (F), *G. Ibarra M. 540* (MO), *G. Ibarra M. & S. Sanaca C. 1776* (MO), *G. Martínez C. 1708* (CAS, F), *R. C. Trigos 198* (F, US), *G. Webster 20895* (TEX); Mpio. Minatitlán, Zona de Uxpanapa, 1–2 km SE of La Chinantla (17°15'30"N, 94°26'30"W), *T. Daniel & T. Wendt 5810* (CAS, CHAPA, MEXU); Mpio. San Andrés Tuxtla, al sur de la Ebrotolotu, *A. Villegas H. 72* (CAS, F, US); Mpio. Hidalgotitlán, desde el Poblado 6, al S por la brecha y la vereda al horcajo oriental del Río Cuevas, 17°15'N, 94°30'W, *T. Wendt et al. 2604* (CAS).

ACKNOWLEDGMENTS

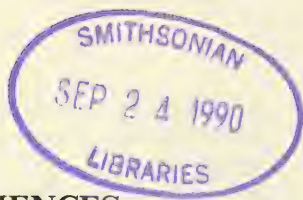
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THREE NEW SPECIES OF
JUSTICIA (ACANTHACEAE) FROM PANAMA

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ABSTRACT: Three new species of *Justicia*, *J. fortunensis*, *J. veraguensis*, and *J. readii*, are described from Panama. The three species are illustrated and their known distributions are mapped. A key to these and a related species in Panama, *J. refractifolia*, is provided. A chromosome number of $n = 14$ is reported for *J. fortunensis*. With 23 species now known from Panama, *Justicia* is the largest genus of Acanthaceae in that country.

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INTRODUCTION

The Acanthaceae of Panama comprise 109 species in 34 genera (Durkee 1988). *Justicia* is the largest and taxonomically most complex genus of Acanthaceae with between 420 (Mabberley 1987) and 600 or so (Graham 1988) species worldwide. Durkee (1988) noted the occurrence of 21 species of *Justicia* in Panama. Recent explorations in the species-rich montane regions near Fortuna Dam and on Cerro Tute in western Panama have resulted in the collection of two undescribed species of *Justicia*. Another species, previously known only from Cerro Jefe, and treated under the name of a species from the Old World, is recognized as new and its range within Panama is expanded.

These three species share several features in

common with *J. refractifolia* (Kuntze) Leonard of Costa Rica and Panama. All four have axillary and terminal inflorescences of conspicuously and densely bracteate spikes with the bracts and corollas less than 20 mm long. These characters distinguish this group of species from all other Panamanian *Justicia*. A key to these four species is presented below.

1. Young stems pubescent with whitish to light brown trichomes (and bracts not drying dark red); calyx pubescent with eglandular trichomes; filaments pubescent.
2. Bracts dark pink (often drying brownish); corolla 8–10 mm long, externally pubescent with glandular and eglandular trichomes; filaments proximally pubescent with eglandular trichomes, dis-

tally glabrous; capsule pubescent with glandular and eglandular trichomes; seeds smooth *J. fortunensis*

2. Bracts green (drying dark green or brown); corolla 10–17 mm long, externally pubescent with eglandular trichomes; filaments pubescent with glandular trichomes throughout length; capsule pubescent with eglandular trichomes; seeds roughened with minute rounded protrusions *J. refractifolia*
1. Young stems glabrous or pubescent with golden trichomes (if trichomes light brown or straw-colored as sometimes in *J. readii*, then bracts drying dark red); calyx pubescent with glandular and eglandular trichomes; filaments glabrous.
3. Young stems glabrous; bracts drying pale to dark greenish; bractlets ovate-elliptic to elliptic to oblanceolate to obovate; calyx 5–6 mm long; corolla 10–13 mm long, externally pubescent with glandular and eglandular trichomes; seeds smooth *J. veraguensis*
3. Young stems evenly covered with a dense layer of (flexuose to 3) antrorse to antrorsely appressed golden (to light brown or straw-colored) eglandular trichomes; bracts drying dark red; bractlets linear-lanceolate to linear to linear-elliptic; calyx 7.5–10 mm long; corolla 15–19 mm long, externally pubescent with eglandular trichomes; seeds papillose to verrucose *J. readii*

Although Leonard (1958) recognized more than 70 species of *Justicia* in Colombia and Durkee (1986) treated 27 species from Costa Rica, none of the taxa from these adjacent regions appears to be conspecific with the three species newly described below. *Justicia* is the largest genus of Acanthaceae in Panama with 23 species now known from the country.

***Justicia fortunensis* sp. nov.**

(Fig. 1)

TYPE.—PANAMA. Chiriquí: vicinity of Fortuna Dam, along trail across valley of Río Hornito, 12 March 1988, T. Daniel, F. Almeda, and G. McPherson 5550 (Holotype: CAS!; isotypes: DUKE!, F!, GH!, K!, MICH!, MO!, NY!, PMA!, US!).

Suffrutex vel frutex usque ad 1 m altus. Caules juniores trichomatibus eglandulosis antrorsis (vel retrorsis) 0.2–0.5 mm

longis in 2 lineis dispositis pubescentes. Folia petiolata, laminae lanci-ellipticae vel ovato-ellipticae vel ellipticae, 45–152 mm longae, 10–56 mm latae, 2.1–5-plo longiores quam latiores. Inflorescentia spicata dense bracteata, rhachis trichomatibus eglandulosis pubescens. Bractae atroseae saepe in sicco brunneolas late ellipticae vel subcirculares vel obovatae 7–13(–17) mm longae 6–11.5 mm latae. Bracteolae ellipticae. Calyx 4.5–6.5 mm longus extus eglandulosus. Corolla 8–10 mm longa extus glandulosa. Stamina 2.8–3 mm longa filamentis pubescentibus. Stylus 4.5–5 mm longus. Capsula 10 mm longa extus glandulosa. Semina 2–3 mm longa 2–2.5 mm lata laevia.

Perennial herb to shrub to 1 m tall. Young stems subquadrate to quadrate, pubescent with antrorse (or retrorse), whitish to light brown (and with conspicuous darker brown septae), eglandular trichomes 0.2–0.5 mm long, mostly concentrated in 2 decussate lines, older stems becoming glabrate. Leaves petiolate, petioles to 14 mm long, pubescent like young stems, blades lance-elliptic to ovate-elliptic to elliptic, 45–152 mm long, 10–56 mm wide, 2.1–5 times longer than wide, acuminate to long-acuminate at apex, acute to attenuate at base, surfaces sparsely pubescent with cauline type trichomes along major veins, otherwise glabrous. Inflorescence of pedunculate, densely bracteate spikes to 60 mm long, 10–20 mm in diameter near midspike, borne singly (or sometimes 2) in axils of distal leaves, peduncles to 45 mm long, pubescent like stems, rachis more or less evenly pubescent with straight to flexuose to antrorse, eglandular trichomes 0.1–0.4 mm long. Bracts dark pink (basal pair rarely somewhat leaflike and partly green), drying pinkish or brownish, broadly elliptic to subcirculate to obovate, 7–13(–17) mm long, 6–11.5 mm wide, rounded or obtuse (and often apiculate) to acute at apex, either abruptly constricted or tapering into a short (to 3 mm long) petiole at base, abaxial surface pubescent with prominent or inconspicuous, straight to flexuose eglandular and stipitate glandular trichomes to 0.5 mm long, margin prominently ciliate with coarse, conspicuously multi-celled, eglandular trichomes to 1.4 mm long. Bractlets elliptic, 6–12 mm long, 1.8–4 mm wide, gradually tapering into a petiole at base, pubescent like bracts. Calyx 4.5–6.5 mm long, 5-lobed, lobes dark pink (at least distally), divided nearly to base of calyx, lanceolate to subulate, 0.5–0.8 mm wide, pubescent with eglandular trichomes. Corolla white to very pale pink, 8–10 mm long, externally pubescent with stipitate glandular and eglandular trichomes 0.1–0.3

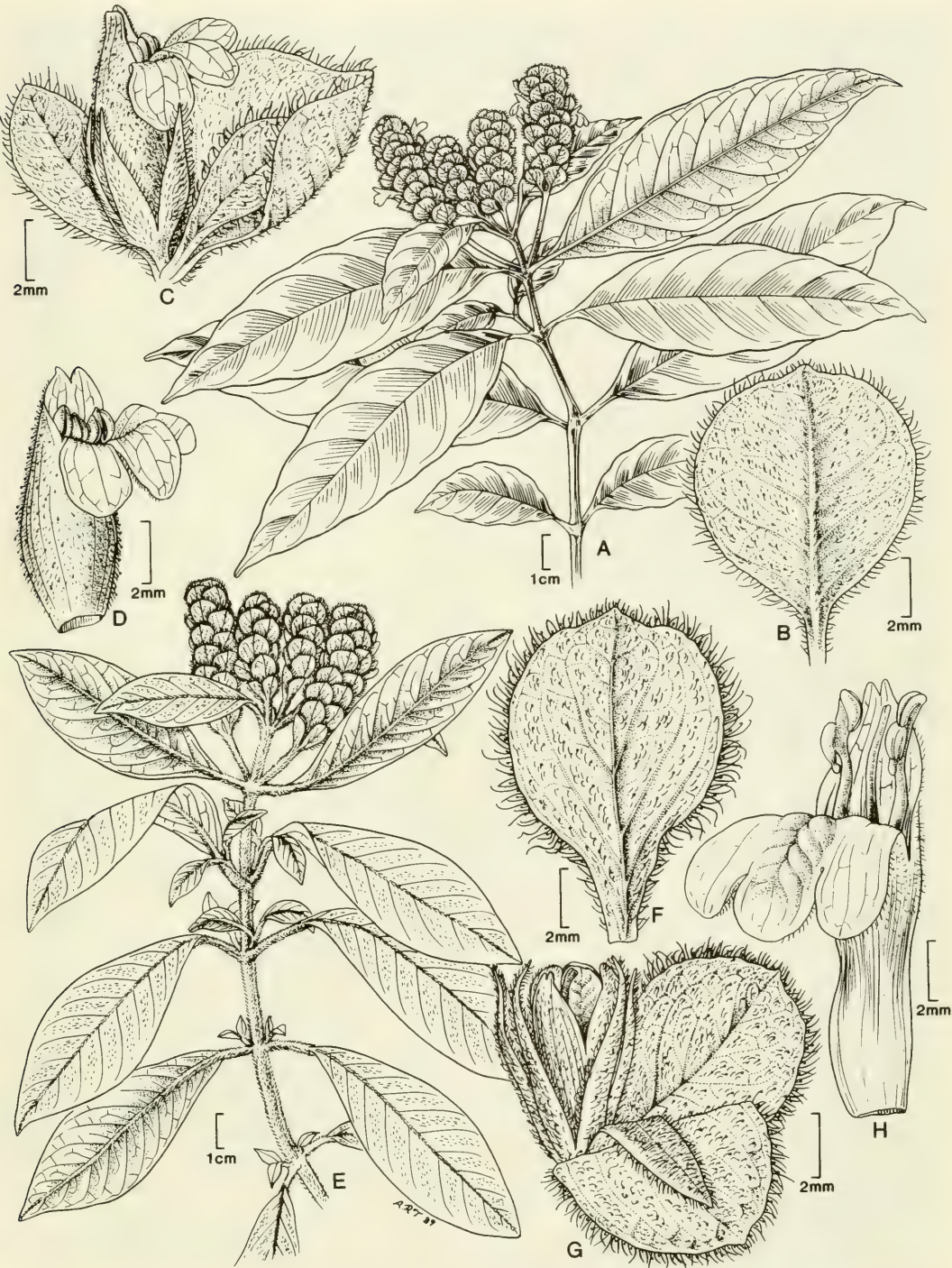


FIGURE 1. a-d, *Justicia fortunensis* (Daniel et al. 5550). a, Habit; b, Bract; c, Bract, bractlets, calyx, and corolla; d, corolla with stamens. e-h, *Justicia readii* (Read et al. 85-6b). e, Habit; f, Bract; g, Bracts, bractlet, calyx, and young corolla; h, corolla with stamens.

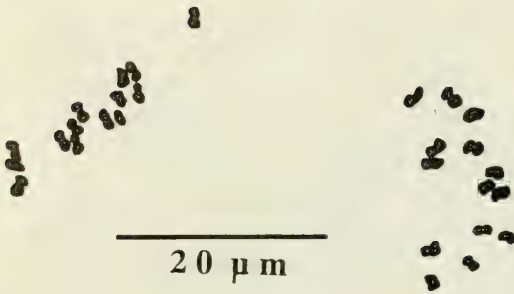


FIGURE 2. Camera-lucida drawing of meiotic chromosomes of *J. fortunensis* (Daniel et al. 5500, $n = 14$) at metaphase II.

mm long, tube 4–5.5 mm long, internally densely pubescent, upper lip triangular, internally rugulate, 3.5–4 mm long with 2 lobes 0.4–0.7 mm long, lower lip 4–4.5 mm long with 3 elliptic lobes 3–3.5 mm long, 2–3.5 mm wide, central lobe larger than lateral lobes. Stamens attached near apex of tube, 2.8–3 mm long, exerted up to 2 mm from mouth of corolla, filaments 1.5–2 mm long, pubescent with eglandular trichomes proximally, glabrous distally, thecae superposed, the upper 1.4–1.5 mm long, the lower 1.5–1.8 mm long (including a blunt basal appendage to 0.2 mm long), pollen diporate (to subdicolporate) with trema region traversed by 2 rows of 6–7

insulae. Style 4.5–5 mm long, distally glabrous, proximally pubescent with upward pointing, eglandular trichomes. Capsule 10 mm long, pubescent with glandular and eglandular trichomes 0.1–0.3 mm long, stipe 4 mm long, head 6 mm long. Seeds 4 per capsule, flattened, subcircular to subelliptic in outline, 2–3 mm long, 2–2.5 mm wide, surface smooth. ($n = 14$, Daniel et al. 5550, Fig. 2)

DISTRIBUTION AND PHENOLOGY.—Known only from Pacific slopes of the Cordillera Central in western Panama (north-central Chiriquí) in the watershed of the Río Chiriquí (Fig. 3). Plants occur in cloud forests at elevations from about 1025 to 1250 m. Flowering: January–April and August; fruiting: January–April.

Justicia fortunensis is not readily identifiable with any subgeneric taxa using the keys and descriptions provided by Graham (1988). It has pollen (“Type 5,” Fig. 4) like that found in five sections recognized by Graham. The chromosome number reported here for the type is the most commonly encountered number in the genus and occurs in various subgeneric taxa (Daniel and Chuang 1989; Daniel et al. 1984, 1990).

The Fortuna Dam area, the only region from which this species is known, has received considerable attention by plant collectors in the last

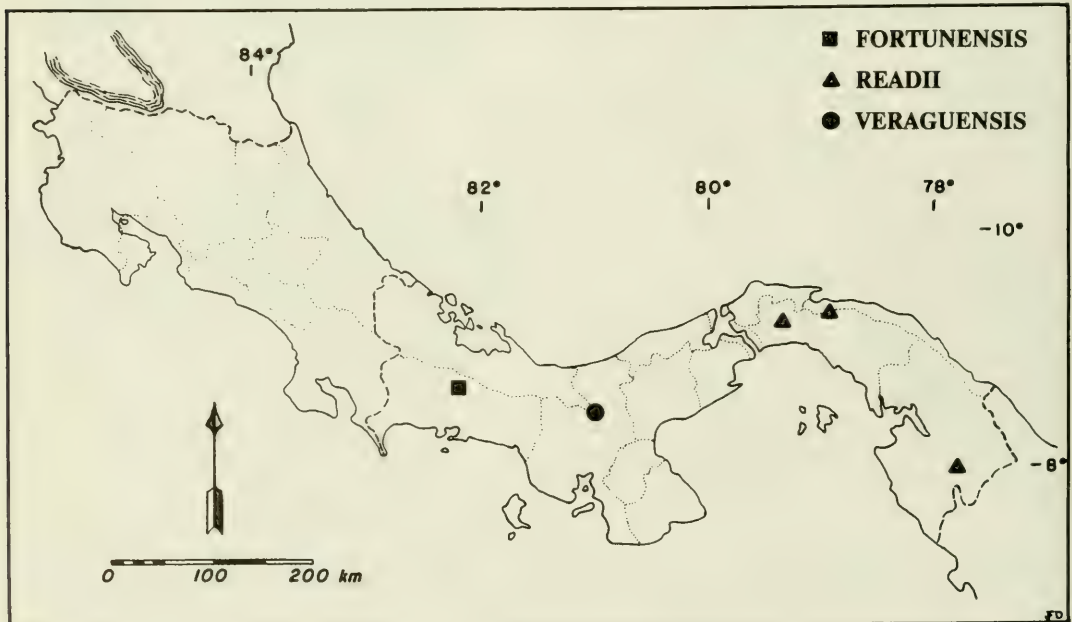


FIGURE 3. Map showing distribution of *Justicia fortunensis*, *J. readii*, and *J. veraguensis*.

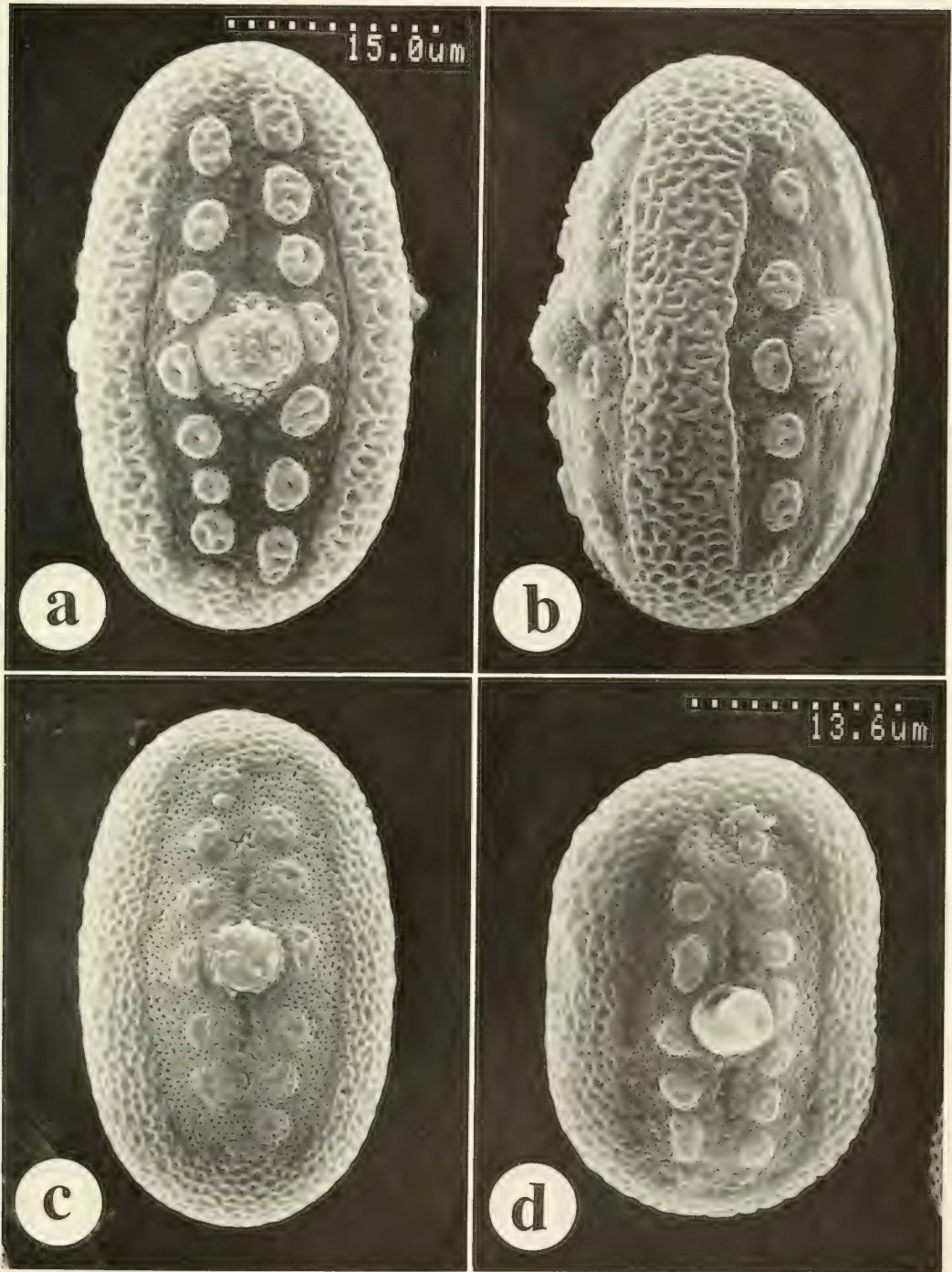


FIGURE 4. Scanning electron micrographs of pollen of *Justicia*. a, *J. readii* (Read et al. 85-6b), view of "trema region"; b, *J. readii* (Read et al. 85-6b), view between 2 "trema regions"; c, *J. veraguensis* (Croat 34153), view of "trema region"; d, *J. fortunensis* (Daniel et al. 5550), view of "trema region."



FIGURE 5. *Justicia veraguensis* (Croft 34153). a, Habit; b, Bract; c, Bractlets, calyx, and gynoecium; d, Corolla with stamens.

few years and has yielded a wealth of new taxa (Dwyer 1985).

PARATYPES.—PANAMA. Chiriquí: Edwin Fabrega Dam and Reserve in Fortuna along trail to Río Hornito above Los Planes, *F. Almeda et al.* 6320 (CAS, MO, PMA, US); W side of Río Hornito, *W. D'Arcy* 16003 (MO); La Fortuna hydroelectric project, along Chiriquí River, *B. Hammel* 2292 (MEXU); between Los Planes de Hornito and Fortuna Lake, 8°41'N, 82°13'W, *R. Hampshire & C. Whiteford* 701 (BM); ca. 5 km

E of Fortuna Dam, along trail crossing Río Hornito, 8°45'N, 82°15'W, *S. Thompson* 5012 (CAS).

***Justicia veraguensis*, sp. nov.**

(Fig. 5)

TYPE.—PANAMA. Veraguas: Cerro Tute, above Santa Fe beyond Escuela Agrícola Inter-americana, 1.8 mi beyond fork in rd., 5 April 1976, *T. Croft* 34153 (Holotype: NY!).

Frutex usque ad 2 m altus. Caules juniores glabri. Folia petiolata, laminae ovato-ellipticae vel ellipticae 65–165 mm longae 21–63 mm latae 2.6–3.4-plo longiores quam latiores.

Inflorescentia spicata dense bracteata, rhachis trichomatibus eglandulosis et plerumque glandulosis pubescens. Bractee in sicco subviridulae vel atroviridulae obovatae vel late ellipticae vel subcirculares vel deltatae 8–13 mm longae 6–8.5 mm latae. Bracteolae ovato-ellipticae vel ellipticae vel oblanceolatae vel obovatae. Calyx 5–6 mm longus extus glandulosus. Corolla 10–13 mm longa extus glandulosa. Stamina 5.5–6 mm longa filamentis glabris. Stylus 8 mm longus. Capsula 9–11 mm longa extus glandulosa. Semina 3–3.3 mm longa 2.7–3.7 mm lata laevia.

Shrub to 2 m tall. Young stems quadrate, glabrous, older stems glabrous. Leaves petiolate, petioles to 50 mm long, glabrous, blades ovate-elliptic to elliptic, 65–165 mm long, 21–63 mm wide, 2.6–3.4 times longer than wide, acuminate at apex, acute to subattenuate at base, surfaces glabrous. Inflorescence of axillary and terminal, pedunculate, densely bracteate spikes to 65 mm long, 13–21 mm in diameter near midspike, peduncles to 15 mm long, glabrous or pubescent in 2 lines with retrorse eglandular trichomes to 0.3 mm long, rachis pubescent with straight to flexuose eglandular and glandular (sometimes not evident) trichomes 0.1–0.3 mm long. Bracts drying pale to dark greenish, obovate to broadly elliptic to subcirculate to deltate, 8–13 mm long, 6–8.5 mm wide, rounded to acute at apex, sessile or petiolate (petiole to 2 mm long), constricted and/or tapering at base, abaxial surface pubescent with straight to flexuose eglandular and glandular trichomes 0.1–0.3 mm long or becoming glabrate, margin ciliate with trichomes like those of abaxial surface and with an overstory of flexuose eglandular trichomes to 1.2 mm long. Bractlets ovate-elliptic to elliptic to oblanceolate to obovate, 6–10 mm long, 1.7–2.7 mm wide, tapering and often petiolate at base, pubescent like bracts. Calyx 5–6 mm long, 5-lobed, lobes divided nearly to base of calyx, lanceolate, 0.7–1.7 mm wide, pubescent like bracts. Corolla white (to greenish white) with purplish markings, 10–13 mm long, externally pubescent with flexuose eglandular and glandular trichomes 0.1–0.3 mm long, tube 6–6.5 mm long, internally glabrous, upper lip triangular, internally rugulate, 4–7 mm long, emarginate with lobes 0.2–0.3 mm long, lower lip 4–7 mm long with 3 broadly elliptic to subcirculate lobes 2.5–4 mm long, 2–4.5 mm wide, central lobe larger than lateral lobes. Stamens attached near apex of tube, 5.5–6 mm long, exerted up to 5 mm beyond mouth of corolla, filaments 4.5–5.2 mm long, glabrous, thecae superposed, the upper 1.2–1.5 mm long, the lower 1.7–2 mm long (including a basal spur

0.3–0.4 mm long), pollen diporate (to subdicolporate) with trema region traversed by 2 rows of 6–7 insulae. Style 8 mm long, distally glabrous, proximally pubescent with eglandular trichomes. Capsule 9–11 mm long, pubescent with glandular and eglandular trichomes 0.1–0.2 mm long, stipe 3.5–4 mm long, head 5.5–7 mm long. Seeds 4 per capsule, flattened, subcircular in outline, 3–3.3 mm long, 2.7–3.7 mm wide, surface smooth.

DISTRIBUTION AND PHENOLOGY.—Known only from the mountains of Veraguas in western Panama. The type and one paratype were collected on the Pacific slopes of Cerro Tute in the Cordillera Central of northern Veraguas (Fig. 3). We have not been able to determine the exact location in Veraguas of the other paratype; however, T. Croat (personal communication) suggests that the Río Segundo Brazo is the second river along the road to the lowlands on the Caribbean slope of Cerro Tute. Plants occur on forested slopes and on rocks in watercourses at elevations from 630 to 1200 m. Flowering: March–April and September; fruiting: April.

Justicia veraguensis exhibits a suite of characters that precludes its placement into any of the sections recognized by Graham (1988). It has pollen (Fig. 4) similar to that of *J. fortunensis*, which is undoubtedly a close relative.

PARATYPES.—PANAMA. Veraguas: 5 mi W of Santa Fe on rd. past Escuela Agrícola Alto Piedra, R. Liesner 852 (GH, MO); Río Segundo Brazo, P. Maas & R. Dressler 1660 (F, U, US).

Justicia readii, sp. nov.

(Fig. 1)

TYPE.—PANAMA. Panamá: Cerro Jefe, 5 January 1972, J. Dwyer 9500 (Holotype: MO!; isotype: NY!).

Frutex usque ad 1.5 m altus. Caules juniores trichomatibus eglandulosis aureis (vel pallidis brunneolis vel stramineis) (flexuosis vel) antrorsis vel appressis 0.4–2 mm longis aequaliter pubescentes. Folia petiolata, laminae ellipticae vel obovatae 45–185 mm longae 17–78 mm latae 2.3–3.8-plo longiores quam latiores. Inflorescentia spicata dense bracteata, rhachis trichomatibus glandulosis et eglandulosis pubescens. Bractee virides in sicco atrovinosae obovatae vel subcirculares vel ellipticae 8–16 mm longae 4.5–11.5 mm latae. Bracteolae lineares-lanceolatae vel lineares vel lineares-ellipticae. Calyx 7.5–10 mm longus extus glandulosus. Corolla 15–19 mm longa extus eglandulosa. Stamina 5–6.5 mm longa filamentis glabris. Stylus 11–16 mm longus. Capsula 9–12.5 mm longa extus glandulosa. Semina 2.3–2.6 mm longa, 2.3–2.5 mm lata papillosa vel verrucosa.

Shrub to 1.5 m tall. Young stems subquadrate to quadrate, densely and evenly pubescent with

(flexuose to) antrorse to antrorsely appressed, golden (to light brown or straw-colored), eglandular trichomes 0.4–2 mm long, older stems remaining pubescent. Leaves petiolate, petioles to 30 mm long, pubescent like stems, blades elliptic to obovate, 45–185 mm long, 17–78 mm wide, 2.3–3.8 times longer than wide, acute to acuminate at apex, acute to attenuate at base, mid-vein pubescent like stems, surfaces sparsely pubescent with similar trichomes. Inflorescence of axillary and terminal, pedunculate, densely bracteate spikes to 75 mm long, 12–21 mm in diameter near midspike, peduncles to 14 mm long, pubescent like stem, rachis pubescent with straight to flexuose (to antrorsely appressed, especially toward base of spike) eglandular and glandular trichomes to 1 mm long. Bracts green, drying dark red, obovate to subcirculate to elliptic, often somewhat asymmetrical, 8–16 mm long, 4.5–11.5 mm wide, rounded and sometimes apiculate to acute at apex, sessile, rounded or constricted and tapering (to subpetiolate) at base, abaxial surface pubescent with straight to flexuose glandular and eglandular trichomes 0.2–0.5 mm long (sometimes not persisting on older bracts), and usually with coarser, antrorse eglandular trichomes to 0.8 mm long as well, margin ciliate with flexuose eglandular (usually coarse) and glandular trichomes up to 2 mm long. Bractlets linear-lanceolate to linear to linear-elliptic, 8–13 mm long, 1.5–2.1 mm wide, tapering little, if at all, and sessile at base, pubescent like bracts. Calyx 7.5–10 mm long, 5-lobed, lobes divided nearly to base of calyx, subulate, 0.5–0.8 mm wide, pubescent with glandular and eglandular trichomes. Corolla whitish to lavender, 15–19 mm long, externally pubescent with flexuose eglandular trichomes to 0.6 mm long, tube 9–12 mm long, internally glabrous, upper lip triangular, internally rugulate, 4.5–8 mm long, emarginate with lobes 0.2–0.3 mm long, lower lip 5–7.5 mm long with 3 subelliptic lobes 2–4.5 mm long, 1.6–2.8 mm wide, central lobe larger than lateral lobes. Stamens attached near apex of corolla tube, 5–6.5 mm long, exerted up to 5.5 mm beyond mouth of corolla, filaments 4–5 mm long, glabrous, thecae superposed, the upper 1.2–1.5 mm long, the lower 1.5–2 mm long (including a basal spur 0.2–0.3 mm long), pollen triporate (to subtricolporate) with trema region traversed by 2 rows of 7 insulae. Style 11–16 mm long, distally glabrous, proximally pubescent with

eglandular trichomes. Capsule 9–12.5 mm long, pubescent with glandular and eglandular trichomes 0.1–0.4 mm long, stipe 3.5–6 mm long, head 5–6.5 mm long. Seeds 4 per capsule, flattened, subcircular in outline, 2.3–2.6 mm long, 2.3–2.5 mm wide, surface papillose (when immature) and papillose to verrucose (when mature).

DISTRIBUTION AND PHENOLOGY.—Cloud forests of eastern Panama (Panamá, San Blas, and Darién) at elevations from 500 to 1300 m (Fig. 3). Flowering November–January; fruiting: December–January.

The type and most other collections of this species have golden, antrorsely-appressed cauline trichomes to 0.8 mm long, relatively small leaves (blades 45 to 90 mm long, 17 to 31 mm wide with petioles to 17 mm long), and relatively short spikes (to 55 mm long) with small bracts (8–12 mm long, 4.5–7 mm wide). Four collections (*Dressler 3221*, *Folsom et al. 6296*, *Maas & Dressler 677*, and *Mori & Kallunki 3424*) differ most conspicuously from those specimens resembling the type by having light brown to straw-colored, flexuose to antrorse-appressed cauline trichomes to 2 mm long, larger leaves (55 to 185 mm long, 18–78 mm wide with petioles to 30 mm long), and somewhat longer spikes (to 75 mm long) with larger bracts (11 to 16 mm long, 5–11.5 mm wide). Although these two forms are readily recognizable, the general overlap in the character states noted above and the occurrence of both in the same region (i.e., Cerro Jefe) suggests that they be treated as a single taxon at this time.

Justicia readii also cannot be classified in Graham's (1988) scheme. It has trilaterally symmetric pollen ("Type 2," Fig. 4) which is characteristic of Graham's section *Tyloglossa* of Africa and Arabia. Species in this section differ from *J. readii* by their inflorescence structure and bract form. In spite of the obvious difference in pollen, *J. readii* is more similar to *J. fortunensis* and *J. veraguensis* than to any other species in Panama.

Durkee (1978) treated this species as *J. adhatoda* L., a widely cultivated species native from the Indian subcontinent to southeastern Asia. *Justicia adhatoda*, which is not presently known from Panama, can be distinguished from *J. readii* by its longer (23–30 mm) corollas; larger (12–34 mm long and 7–12 mm wide) and eglandular bracts that do not dry dark red; linear-elliptic,

eglandular, and wider (1.5–2.3 mm) calyx lobes; longer (3.5–4.5 mm) thecae, both of which bear basal spurs; and bilaterally symmetric pollen.

Justicia readii has been rather well collected on Cerro Jefe, a mountain northeast of Panama City that has been much visited since it became readily accessible to plant collectors in the mid-1960's (Dwyer 1967, 1985). It is not surprising that the species was recently collected along the relatively new El Llano-Cartí Road in the Serranía de San Blas. There is a continuous ridge system linking Cerro Jefe with the Serranía de San Blas. The southeasternmost station for this species, in the Serranía de Pirre in Darién, is rather isolated from the other known occurrences.

PARATYPES. — PANAMA. Darién: ridgetop area N of Cerro Pirre, between Cerro Pirre top and Rancho Plastico, *J. Folsom et al.* 6296 (MO). Panamá: Cerro Jefe, along main rd. before turn-off to summit, *T. Croat* 13054 (MO); La Eneida, region of Cerro Jefe, *R. Dressler* 3221 (MO); Cerro Jefe, *J. Dwyer & A. Gentry* 8489 (MO); near top of Cerro Jefe to 1 mi. beyond, *A. Gentry et al.* 3440 (MO); La Eneida, Cerro Jefe region, *P. Maas & R. Dressler* 677 (MO); 5–10 km NE of Altos de Pacora, "Campamento Quatro," Gorgas Memorial Labs yellow fever research camp, *S. Mori & J. Kallunki* 3424 (MO, NY); Cerro Jefe, near jct. of rds. to Cerro Jefe and Altos de Pacora, *S. Mori et al.* 3776 (MO); rd. from Cerro Jefe to Cerro Azul, *E. Tyson* 5306 (MO); Cerro Jefe between Cerro Azul and La Eneida, ca. 15 mi NE of Panama City, *R. Wilbur et al.* 15541B (DUKE, MO). San Blas: Serranía de San Blas, Nusagandí along El Llano-Cartí Rd., *R. Read et al.* 85-6B (US).

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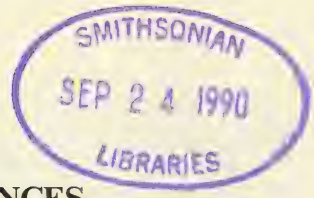
RESUMEN

Se describen e ilustran tres especies nuevas de *Justicia* de Panamá: *J. fortunensis*, *J. veraguensis*, y *J. readii*. Se presenta un mapa que muestra la distribución de cada una de las especies. Las tres especies nuevas parecen tener afinidades con *J. refractifolia* y una clave de estas cuatro especies es presentada. Se reporta un número de cromosomas de $n = 14$ para *J. fortunensis*. Con 23 especies en el país, *Justicia* es el género mas grande de Acanthaceae en Panamá.

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NEW SPECIES AND NEW COMBINATIONS IN *BLAKEA* AND
TOPOBEA (MELASTOMATACEAE), WITH AN HISTORICAL
PERSPECTIVE ON GENERIC LIMITS IN
THE TRIBE BLAKEEAE

By

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ABSTRACT: *Blakea* P. Browne and *Topobea* Aublet, the two currently recognized genera in the Blakeeae have been variously combined and segregated during their long history. A synoptic taxonomic history of these genera is presented with special attention given to characters used to combine or separate them. In keeping with traditional generic concepts, *Blakea* and *Topobea* are maintained and a revised generic key is provided to accommodate anomalous or unusual Mesoamerican species. Descriptions, diagnostic illustrations, discussions, and distribution maps are presented for four new species of *Blakea* (*B. gregii*, *B. hammelii*, and *B. herrerae* from Panama; and *B. scarlatina* from Costa Rica and Nicaragua) and three new species of *Topobea* (*T. fragrantissima*, *T. hexandra*, and *T. suaveolens* from Panama). The study of recently collected flowering material of *B. crassifolia* and *B. parvifolia* necessitates their transfer to *Topobea* and the adoption of a new name, *T. caliginosa*, for the narrow Panamanian endemic previously known as *B. micrantha*.

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INTRODUCTION

The largely pantropical Melastomataceae comprise some 200 genera and approximately 4,800 species. This comparatively large natural family has traditionally been divided into fourteen tribes based on fruit characters, staminal features, and seed morphology. Of the eight tribes restricted to the western hemisphere, only the Blakeeae and Miconieae are berry-fruited. The Blakeeae are readily recognized by their axillary flowers that are individually subtended by two pairs of decussate bracts, ovoid to pyramidal smooth seeds, and wood with multiseriate rays and frequent occurrence of druses (Koek-Noorman et al. 1979; ter Welle and Koek-Noorman 1981).

The striking morphological isolation of the Blakeeae within the family and the homogeneity of its constituent taxa undoubtedly account for the fact that its tribal status has not been seriously challenged since it was established by Bentham and Hooker (1867). However, *Blakea* P. Browne and *Topobea* Aublet, the two currently recognized genera in the tribe, have been variously combined and segregated during their long history.

Recent fieldwork done in connection with the preparation of a treatment of Melastomataceae for Flora Mesoamericana has resulted in the discovery of several undescribed species in the Blakeeae. An effort to devise a rational basis for assigning these taxa to one genus or the other has necessitated another look at generic limits in the

tribe. I recently expressed serious reservations about the continued recognition of *Topobea* and even suggested that it be submerged in the older and larger genus *Blakea* (Almeda 1989). Additional study of this problem, coupled with the paucity of information on pollen morphology (Patel et al. 1985) and chromosome numbers (Solt and Wurdack 1980), has led me to refrain from merging *Blakea* and *Topobea* without a comprehensive study throughout the extensive neotropical range of these genera.

The following summary provides a synoptic taxonomic history of *Blakea* and *Topobea* together with an assessment of the diagnostic features used to combine or separate them. This is followed by descriptions of four new species of *Blakea*, three new species of *Topobea*, and three generic transfers. Working within the constraints of a geographically defined study, my decision to recognize *Blakea* and *Topobea* is, of necessity, tempered by the historical consensus of opinion among specialists in the family and the need for more data. Nevertheless, a slight modification of original generic concepts is necessary to accommodate the accretion of new and unusual Central American species.

SYNOPTIC HISTORY OF *BLAKEA* AND *TOPOBEA*

The genus *Blakea* was first defined by Patrick Browne (1756) for a Jamaican species that was subsequently given the binomial *B. trinervia* by Linnaeus (1759). Browne's circumscription of *Blakea* included a plate and a brief diagnosis describing it as a shrub with nitid trinerved elliptic leaves, 6-merous axillary flowers, and triangular laterally connate anthers. The plate is generalized and provides no details of anther morphology. The terse description is sufficient, however, to preclude confusion with the allied genus *Topobea*, which was described and illustrated by Aublet (1775) from material collected in French Guiana. Although many of Aublet's published drawings are mixtures and some of his descriptions are composites of discordant elements (Howard 1983), both the plate and description of *T. parasitica* emphasize the oblong subulate anthers that are typical of so many species in this genus. Curiously, Aublet overlooked or chose not to describe and illustrate the broad, gaping, dorsally inclined, confluent anther pores. This is another diagnostic character that

figures prominently in decisions to maintain *Topobea* as a distinct genus. In choosing the epithet *parasitica*, Aublet was responsible for perpetrating a misunderstanding of the epiphytic habit that is common to so many species of *Blakea* and *Topobea*.

The younger Linnaeus (1781) and de Jussieu (1789) maintained *Blakea* and *Topobea* as defined by Aublet. By retaining *Blakea quinque-nervia* Aublet [= *Bellucia grossularioides* (L.) Triana] in *Blakea*, it is clear that their interpretation was a broad one that included at least two genera now relegated to two different berry-fruited tribes.

David Don (1823), in an early paper devoted to the Melastomataceae, was the first to part ranks with his predecessors by merging *Topobea* and *Blakea*. His decision, however, was based on characters other than anther morphology. The weakness of Don's argument is best conveyed by his own words: "Although the *Topobea* of Aublet recedes somewhat from *Blakea*, in its being parasitical; yet, notwithstanding, in the Lambertian Herbarium are several unpublished species, from Don Jose Pavon, natives of Peru, and not parasitical, which agree with *Topobea* in every essential point; and these also, accord well with *Blakea*, except in having four, instead of six scales, surrounding the calyx, which, however, is a variable character; and, therefore I think myself justified in uniting these two genera." De Candolle (1828) also adopted this interpretation in his *Prodromus*. Like Don and his immediate predecessors, de Candolle's broad generic concept of *Blakea* included species now recognized in *Bellucia*.

Naudin (1852) rejected this inclusive disposition and emphasized diversity in anther morphology and habit as reasons for resurrecting *Topobea*. He provided no involved explanation to justify his decision, yet he described a new genus, *Pyxidanthus*, to accommodate three new species that he considered closely related to *Blakea*. The concept of *Blakea* and *Topobea* espoused by Naudin was faithfully followed by Bentham and Hooker (1867) without comment.

Triana (1871), as astute specialist in the Melastomataceae, synonymized *Pyxidanthus* under *Blakea* along with *Valdesia* Ruiz and Pavon, another minor generic segregate. *Pyxidanthus*, *Valdesia*, and the subsequently described *Amaraboya* Linden are now universally accepted synonyms of *Blakea*. As recognized by Triana (1871),

Blakea included those species with short, oval or elliptic, apically blunt or rounded anthers with two minute well-separated pores. *Topobea* included those species with linear-oblong or subulate anthers with two confluent dorsally inclined pores. Baillon (1879), who was noted for his broad view of generic limits, was unimpressed by these differences in anther morphology. He returned *Topobea* to the synonymy of *Blakea* but provided no convincing reasons aside from a comment describing the anthers of *Topobea* as more elongate and narrower than those in *Blakea*. For a botanist who excelled in character analysis, Baillon's brief treatment of these genera reflects a superficial understanding of the anther differences between them.

The most comprehensive and perhaps most influential accounts of generic limits in the Blakeae are those of Cogniaux (1888, 1891). Cogniaux was undoubtedly influenced by Triana. Unlike Triana, however, he was the first to provide the following explicit key clarifying the distinctions between *Blakea* and *Topobea* as he understood them:

- A. Stamina filamenta crassiuscula, antherae breves, obtusae a latere compressae, connectivo crassissimo, postice calcarato *Blakea*
- B. Stamina filamenta filiformia; antherae lineari vel oblongo-subulatae, rostratae, connectivo mediocri, interdum ecalcarato *Topobea*

These differences amply characterized the species then known to Cogniaux, but they cannot be used for a strict characterization of the two genera at present. The short, obtuse, laterally compressed anthers of *Blakea* (Fig. 2A, C, E; Fig. 3A, E) versus the linear to oblong-subulate rostrate anthers of *Topobea* (Fig. 1E, F; 2B; 3B, C) are the only modal contrasts that appear to be valid for distinguishing the majority of species now assigned to these genera. The differences in filament thickness and presence or absence of dorsal appendages on the connective are inconsistent criteria for differentiating *Blakea* and *Topobea*. Like his predecessors, Cogniaux neglected to emphasize that *Blakea* has anthers with two typically minute and well-separated pores and *Topobea* has two (rarely one) broad approximate or confluent dorsally inclined pores. The generic concepts promoted by Cogniaux have been adopted by all subsequent specialists (Almeda,

in press; Gleason 1935, 1958; Wurdack 1973, 1980) and other authors of major regional treatments of the Melastomataceae (Standley 1924, 1938; Standley and Williams 1963), except Macbride (1941). Invoking a rationale similar to that of Baillon, Macbride combined *Blakea* and *Topobea* and commented on the inconsistency of the filament character used as a diagnostic feature by Cogniaux.

In a paper describing many new species of *Blakea* and *Topobea*, Gleason (1945) sympathized with, but rejected, Macbride's view. The close relationship between these two genera is readily apparent in their many parallel and overlapping variations in habit, leaves, indument, floral bracts, petals, calyx lobes, ovary cell number, and seeds. Although Baillon (1879) and Macbride (1941) intimated that anther characters provide insufficient grounds on which to base the recognition of genera, Gleason (1945, 1947), who defended their use, pointed out that specimens can be sorted precisely into one genus or the other when staminal material is available.

According to Patel (in litt., 18 July 1985), preliminary results of a numerical taxonomic analysis of pollen (using SEM data) in the Melastomataceae reveal that *Blakea* and *Topobea* sort out into different clusters. Because pollen of Melastomataceae is diverse exomorphically (Patel et al. 1985), an expanded survey is needed to extend and refine these observations.

Until more information about micromorphological characters such as chromosome numbers, pollen morphology, and chemistry is available, it seems preferable to adhere to traditional generic concepts until we can rest decisions on a broader data base than was available to our predecessors.

This, however, does not ease the current difficulty of assigning the few unusual species to one genus or the other. In the Mesoamerican region, at least four different species groups are problematic in determining where to draw the line between *Blakea* and *Topobea*. I will consider the relationships among *Blakea wilburiana* Almeda and allied species in a future paper. The other three species groups are mentioned here because at least one species from each is newly described below.

The first of these, *Blakea gregii*, belongs to a group of five closely related species characterized by nectar-producing pendant flowers with green petals. The anthers of *B. gregii* are elliptic-oblong

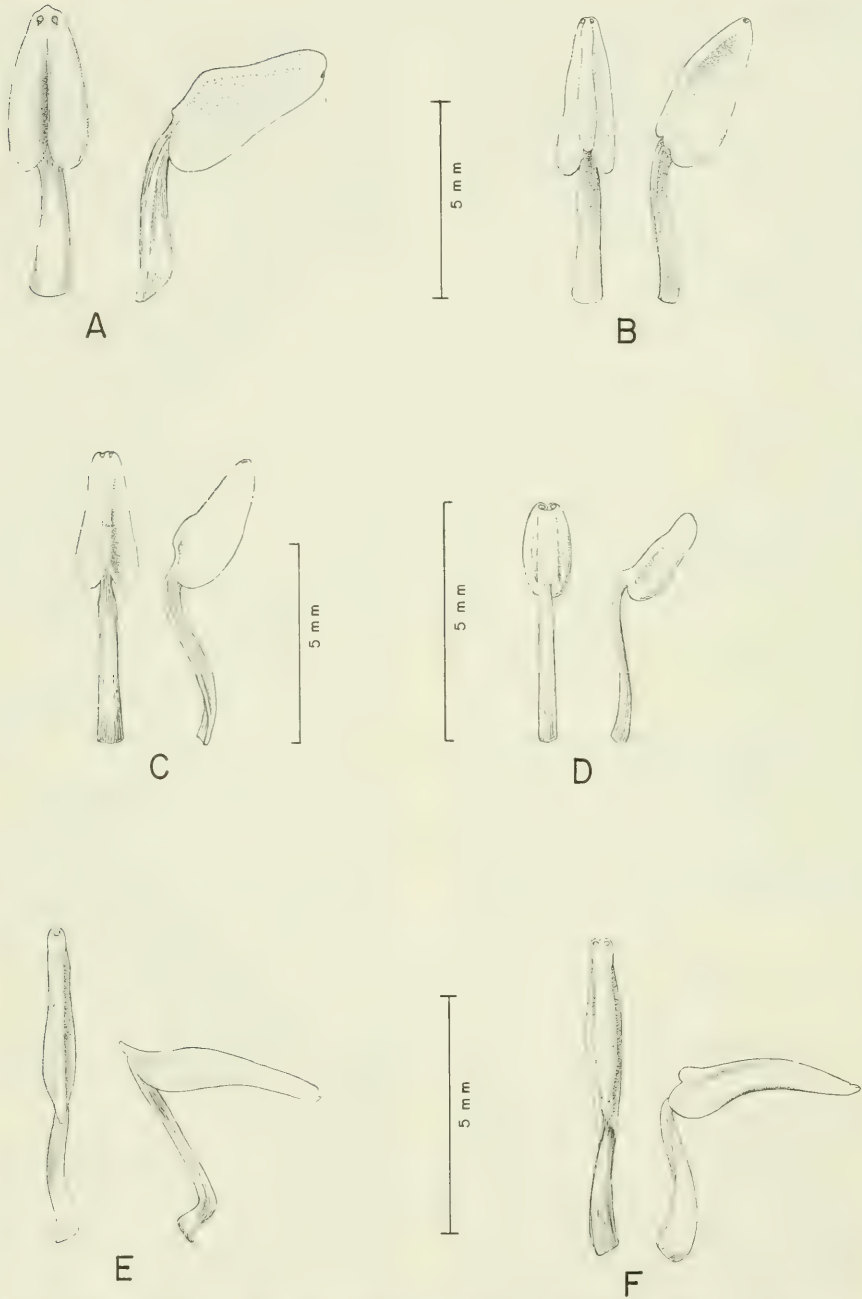


FIGURE 1. Representative stamen morphology in *Blakea* and *Topobea*. A, *B. wilburiana* Almeda; B, *B. austin-smithii* Standley; C, *B. purpusii* Brandegee; D, *T. crassifolia* (Almeda) Almeda; E, *T. pittieri* Cogn.; F, *T. brenesii* Standley. (A from Almeda et al. 6525, CAS; B from Almeda et al. 2145, CAS; C from Breedlove & Almeda 47747, CAS; D from de Nevers 5943, CAS; E from Almeda et al. 3161, CAS; F from Wilbur et al. 15809, DUKE.)

and laterally compressed with two dorsally inclined approximate pores (Fig. 4G). Anther conformation is like that of *Blakea* but the dorsal inclination of the apical pores is more like that

encountered in *Topobea*. The pore width, however, is narrower than that typically found in many species of the latter genus. In deciding to place this species in *Blakea*, I was influenced by

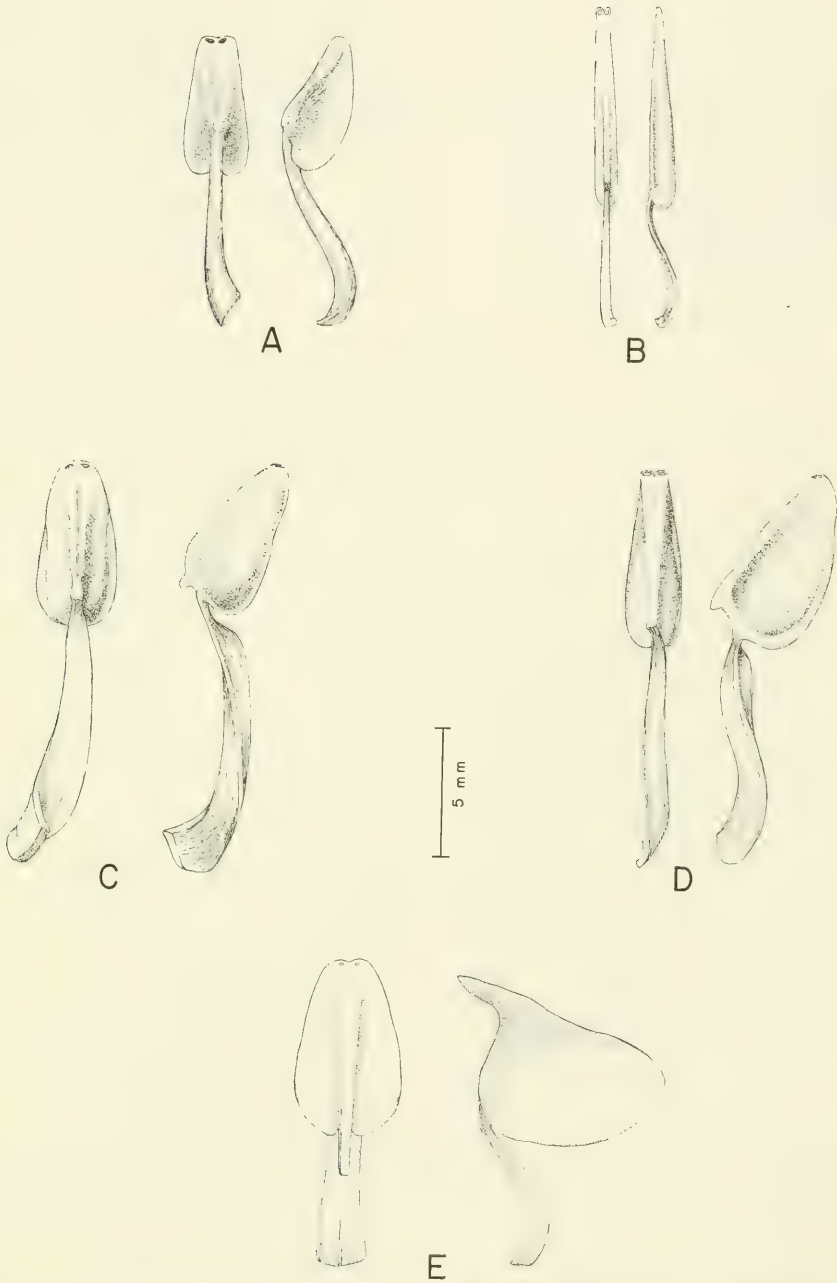


FIGURE 2. Representative stamen morphology in *Blakea* and *Topobea*. A, *B. elliptica* (Gleason) Almeda; B, *T. calycularis* Naudin; C, *B. woodsonii* Gleason; D, *T. storkii* Standley; E, *B. tuberculata* J. D. Smith. (A from Almeda *et al.* 6261, CAS; B from Breedlove 50940, CAS; C from Almeda *et al.* 3046, CAS; D from Almeda *et al.* 2884, CAS; E from Almeda & Nakai 4529, CAS.)

the somewhat more typical *Blakea*-type anthers of its close relatives, *B. austin-smithii* Standley (Fig. 1B) and *B. purpusii* Brandegee (Fig. 1C).

Topobea hexandra has been the most difficult

to place generically. It is part of an unusual assemblage in the *Blakeeae* distinguished by small sessile or short-pedicellate flowers with only six antesealous stamens. Its close relatives include

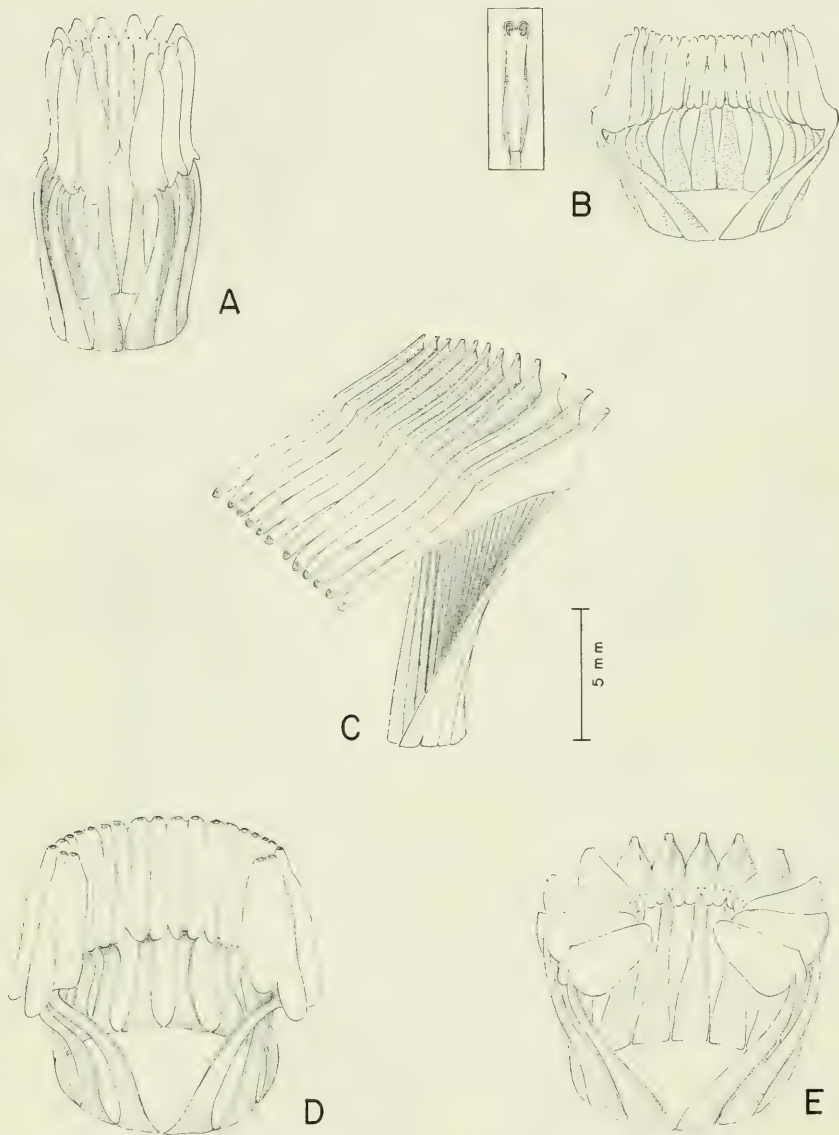


FIGURE 3. Representative stamen morphology in *Blakea* and *Topobea*. A, *B. litoralis* L. O. Williams; B, *T. parvifolia* (Gleason) Almeda; C, *T. albertiae* Wurdack; D, *B. hirsuta* Triana var. *rotundata* Markgraf; E, *B. anomala* J. D. Smith. (A from Almeda & Nakai 4189, CAS; B from Almeda et al. 5898, CAS; C from Almeda et al. 6153, CAS; D from Lugo 4140, CAS; E from Almeda 2655, CAS.)

T. cordata Gleason, *T. caliginosa* Almeda, and *T. crassifolia* (Almeda) Almeda. Stamens of *T. cordata* were unknown to Gleason (1950) when he proposed it as a new species. His decision to place it in *Topobea* was based on its superficial resemblance to some sessile-leaved species of that genus. Although each of the species in this complex is known from very few flowering collec-

tions, available anther material exhibits interesting variations on the *Topobea* theme. With the exception of *T. hexandra*, all have anthers with two broad confluent pores. In *T. cordata*, the anthers are oblong-subulate (5–5.5 mm long) and the confluent pores are somewhat ventrally inclined. In *T. caliginosa* and *T. crassifolia* the anthers are linear-oblong but shorter (2–2.5 mm)

with truncate to somewhat dorsally inclined pores (Fig. 1D). The anthers of *T. hexandra* are also short (2 mm) and oblong, but they are laterally compressed and the two apical pores, although broad, are ventrally inclined and separated from one another (Fig. 11F). In the context of variation exhibited by its close relatives, the summation of anther characters in this species argues for placement in *Topobea*. Without these insights, one might be inclined to assign it to *Blakea*.

The last of the problematic species to be considered here is *T. suaveolens* Almeda. This species is unusual in having fragrant pendant flowers with brightly colored petals and connivent anthers that form a ring around the exerted style (Fig. 12C). The essentially elliptic shape and conspicuous lateral compression of the anthers (Fig. 12E) are reminiscent of *Blakea*-type anthers but the broad solitary dorsally inclined apical pore is a feature known only in *Topobea*. Again, my generic placement of this species is influenced by its close relationship to *T. fragrantissima* Almeda (Fig. 10), a species with androecial characters that can only be attributed to *Topobea*.

Interestingly, the anomalous androecial morphology in the cases discussed above all appear to represent derived syndromes. Each is associated with a unique pollen presentation mechanism (*T. suaveolens*), a specialized pollinator spectrum (see discussion under *B. gregii*), or great reduction in flower size (*T. hexandra*). *Blakea*, with about 100 described species, and *Topobea*, with over 60 species, are large and diverse, closely related genera. If more unusual anther forms come to light, it may become increasingly difficult to separate them without establishing arbitrary limits or fueling counterarguments to submerge *Topobea*. For floristic purposes, I find it expedient to recognize both genera. This is done for convenience and to preclude extensive nomenclatural changes pending a comprehensive study of the tribe. It is not done out of a firm conviction that generic status is necessarily the best way to reflect relationships based on currently perceived differences. Accordingly, the following revised key to these genera is offered in an attempt to incorporate the most obvious Mesoamerican anomalies discovered to date:

Stamens 12 in number; anthers 2-pored, oval, oblong, or elliptic, compressed laterally, bluntly obtuse or broadly rounded at the

summit with two typically well-separated (often minute) apical pores *Blakea*
Stamens 6, 8, or 12 in number; anthers 1-pored or 2-pored, linear-oblong to oblong-subulate or rostrate, usually not compressed laterally (if conspicuously compressed then 1-pored or dorso-basally appendiculate) with approximate or confluent dorsally inclined pores (if pores are prominently inclined ventrally then flowers are hexandrous or pedicels are beset with spreading brown hairs 1–2.5 mm long) *Topobea*

NEW TAXA AND NEW COMBINATIONS

***Blakea gregii* Almeda, sp. nov.**

(Fig. 4)

TYPE:—PANAMA. Chiriquí: Cerro Pate Macho, windswept ridge, 8°49'N, 82°24'W, elev. 2,100 m, 17 Jan. 1986, *de Nevers & McPherson 6840* (holotype: CAS! isotypes: MEXU!, MO!, PMA!, US!).

Frutex ca. 2–4 m altus. Ramuli primum quadrangulati demum teretes sicut petioli laminarum subtus pedicelli bracteaeque pilis 1–2.5 mm longis induti. Petioli 1.8–3.5 cm longi; lamina 9.3–14.5 × 5–9 cm elliptica vel elliptico-ovata apice acuminata basi obtusa vel rotundata vel late acuta, 5-nervata vel 5-plinervata, coriacea et integra, nervis secundariis 3–6 mm inter se distantibus. Flores 6-meri penduli in quoque nodo superiore plerumque 1–4, pedicellis 1.2–2 cm longis; bractae exteriores 7–8 × 5–8 mm ellipticae vel ovato-ellipticae ad basim paulo (2 mm) coalitae; bractae interiores omnino liberae 5–6 × 4–7 mm ovatae vel suborbiculares apice truncato-rotundatae. Hypanthium (ad torum) 6 mm longum extus glabrum vel sparse subamorpho-furfuraceum; calycis tubus 2–3 mm longus, lobis 2–4 mm longis extus sparsiuscule strigosus. Petala 13–14 × 9–11 mm obovata apice rotundata sparse caduceque glanduloso-ciliolata. Filamenta 6–7 mm longa; antherae 4–4.5 × 2 cm subulatae lateraliter non cohaerentes, dorsaliter biporosa; connectivum dorsaliter ca. 0.5 mm supra thecarum basim inconspicue tuberculatum. Stylus 1.2–1.3 cm; ovarium 6-loculare et ½ inferum apice glabro (cono et collo non evoluto).

Terrestrial shrubs 2–4 m tall. Young internodes quadrate, becoming rounded with age. Distal branchlets, vegetative buds, petioles, and pedicels densely covered with a brown indument of appressed, ± curved subulate hairs mostly 1–2.5 mm long. Mature leaves of a pair essentially equal in size; petioles 1.8–3.5 cm long; blades coriaceous, 9.3–14.5 cm long and 5–9 cm wide, elliptic to elliptic-ovate, apex acuminate, base obtuse to rounded but sometimes varying to broadly acute, margin entire and somewhat revolute when dry, 5-nerved or 5-plinerved, the innermost pair of primaries diverging from the median nerve 4–6 mm above the blade base, the

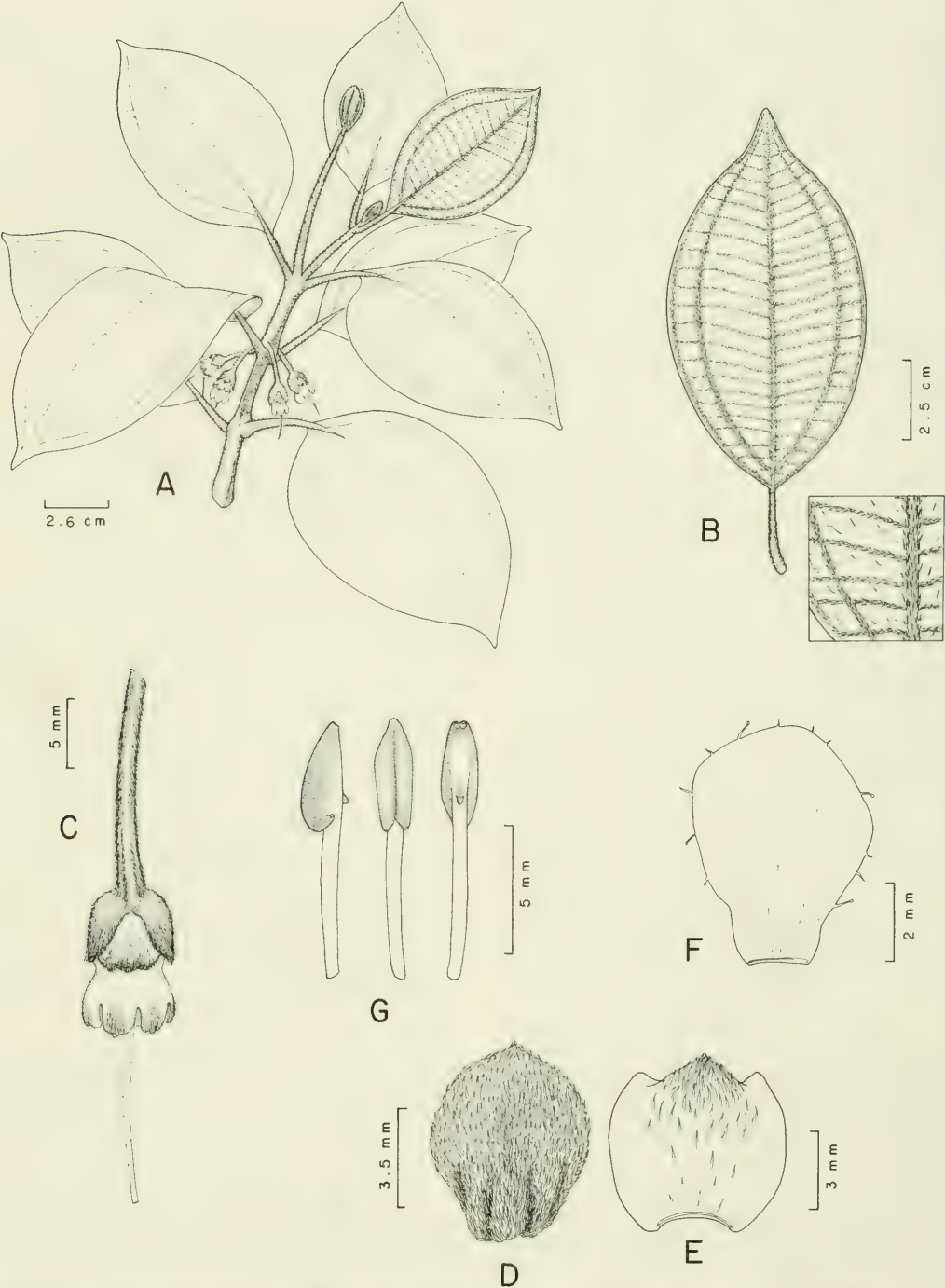


FIGURE 4. *Blakea gregii* Almeda. A, habit; B, representative leaf with enlargement (abaxial surface); C, representative flower (natural posture) with petals and stamens removed; D, outer floral bract (abaxial surface); E, inner floral bract (abaxial surface); F, petals (adaxial surface); G, stamens, lateral view (left), ventral view (middle), dorsal view (right). (A from *Almeda et al.* 6137, CAS; B-G from the holotype.)

elevated network of transverse secondaries spaced 3–6 mm apart at the widest portion of the blade, the young unexpanded leaves beset with a deciduous indument of white wooly hairs but typically becoming glabrous adaxially at maturity and moderately to copiously covered abaxially with smooth appressed to $\pm$ curved brown hairs 1.5–2.5 mm long. Flowers pendant, solitary, paired, or in fascicles of 4 in the leaf axils of distal branches; pedicels 1.2–2 cm long. Floral bracts thick and semisucculent, sessile and entire; outer bracts connate basally for 2 mm, 7–8 $\times$ 5–8 mm, elliptic to elliptic-ovate, apex acute, densely covered abaxially with appressed to incurved smooth brown hairs; inner bracts free to the base, 5–6 $\times$ 4–7 mm, ovate to subrotund, apex rounded to truncate varying to retuse with a bluntly acute median lobe, sparingly to moderately beset with appressed brown hairs that are typically concentrated around or restricted to the median apex. Hypanthia (at anthesis) campanulate to suburceolate, 6 mm long to the torus and 7–8 mm in diameter, glabrous or sparingly brown furfuraceous toward the base. Calyx tube 2–3 mm long; calyx lobes erect, 2–4 mm long and 4–5 mm wide basally, ovate to deltoid-ovate with a blunt callose-thickened tooth at the abaxial apex of each lobe, roughened along interlobe sinuses, adaxially glabrous, abaxially covered with a sparse indument of tardily deciduous short incurved brown hairs that are restricted to or largely concentrated near the apex. Petals 6, glabrous, connivent to somewhat imbricate when fully expanded, 13–14 $\times$ 9–11 mm, green, obovate, apically rounded, entire but irregularly glandular-ciliate. Stamens 12, isomorphic, free and encircling the exerted style; filaments complanate and glabrous, 6–7 mm long; anthers 4–4.5 mm long, 2 mm wide, elliptic-oblong, laterally compressed, each anther tipped with two dorsally inclined approximate pores; connective dilated dorso-basally ca. 0.5 mm above the filament insertion into a blunt callose spur. Ovary $\frac{1}{2}$ inferior, 6-celled, glabrous and lobulate at the apex but not expanded into a cone or collar. Style straight, glabrous, 1.2–1.3 cm long, conspicuously exerted beyond the petals and calyx lobes; stigma truncate. Berry globose, about 6 mm long and 8 mm in diameter. Seeds clavate to narrowly pyriform, ca. 1 mm long, beige with a smooth glossy testa and a conspicuous lateral raphe.

PHENOLOGY.—Flowering specimens have been

collected in January; the only fruiting specimen was collected in March.

DISTRIBUTION.—A little-collected cloud forest or elfin forest species known only from Chiriquí Province, Panama in the region extending from Cerro Horqueta to Cerro Pate Macho at 1,800–2,200 m (Fig. 5).

ADDITIONAL SPECIMENS EXAMINED.—PANAMA. Chiriquí: S slopes of Cerro Horqueta, 21 Jan. 1971, *Wilbur et al.* 13486 (CAS, DUKE, MO); Cerro Pate Macho, 8°49'N, 82°24'W, 13 Mar. 1988, *Almeda et al.* 6137 (CAS, CR, MO, NY, PMA, TEX).

Blakea gregii is closely related to four other species characterized by cryptic, pendant flowers with green, connivent petals and nocturnal or crepuscular nectar production (Almeda 1980, 1981a). The green-flowered species are typically cloud forest hemiepiphytes that germinate terrestrially, ascend nearby trees by adventitious roots, and ultimately become epiphytic by losing root contact with the soil. Both *B. chlorantha* and *B. gregii*, however, are often conspicuous terrestrial shrubs on windswept ridges of the continental divide where the vegetation is commonly reduced to elfin woodland.

Intensive field studies by Lumer (1981) and Lumer and Schoer (1986) have shown that *B. austin-smithii*, *B. chlorantha*, and *B. penduliflora* are visited and pollinated by six species of rodents belonging to four genera: *Oryzomys*, *Peromyscus*, *Reithrodontomys*, and *Scotinomys*. Lumer and Schoer (1986) suggest that rodents may indeed play a significant role as pollinators of flowering plants in the harsh windy cloud forest environment. Nothing is known about the pollination of *B. gregii*, but similarities in floral morphology and habitat suggest that small rodents may also play an important role in the reproductive biology of this species.

To facilitate comparison, diagnostic characters of the five species of *Blakea* with pendant green flowers are summarized in the following key:

1. Leaf blades modified adaxially at the petiole-laminar junction into flap-like saccate pouches, the basal and lateral margins of which are free from but conspicuously decurrent on the petiole.
2. Pubescence of uppermost internodes consisting of hairs 1–2 mm long; leaf blades bluntly denticulate and revolute on drying; outer floral bracts linear-lan-

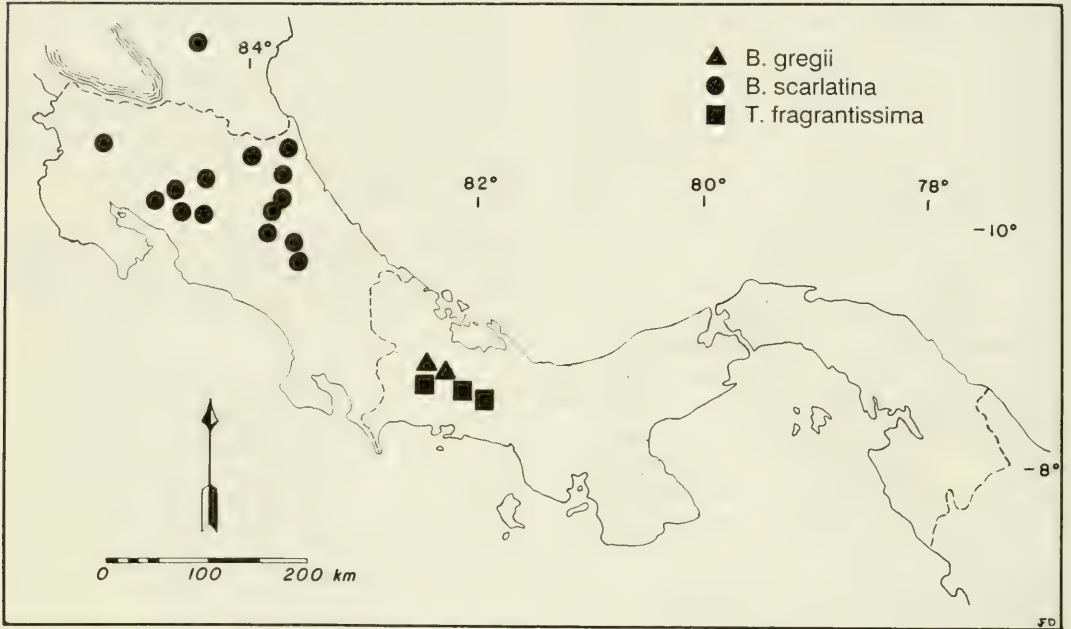


FIGURE 5. Distributions of *Blakea gregii*, *B. scarlatina*, and *Topobea fragrantissima*.

ceolate, 15–21 mm long, equaling or exceeding the calyx lobes at anthesis; Costa Rica (Cerro Chompipe, Volcán Barva, and Volcán Irazú)

..... *B. austin-smithii* Standley

2. Pubescence of uppermost internodes consisting of hairs mostly less than 0.5 mm long; leaf blades entire and revolute on drying; outer floral bracts ovate to elliptic-ovate, 5.5–9 mm long, conspicuously shorter than the calyx lobes at anthesis; Costa Rica (Cordillera de Tilarán) *B. chlorantha* Almeda

1. Leaf blades not modified adaxially at the petiole-laminar junction into flap-like saccate pouches.

3. Older petioles, pedicels, and floral bracts essentially glabrous; outer floral bracts 13–17 mm wide on fruiting hypanthia; Costa Rica (Cordillera de Talamanca and Volcán Barva)

..... *B. penduliflora* Almeda

3. Older petioles, pedicels, and floral bracts moderately to copiously covered with appressed or spreading brown hairs; outer floral bracts 5–9 mm wide on fruiting hypanthia.

4. Uppermost internodes and elevated

primary nerves on lower leaf surfaces moderately to densely covered with spreading brown hairs mostly less than 0.5 mm long; pedicels (20–) 28–38 mm long; outer floral bracts 13–20 mm long; Mexico (Chiapas) and western Guatemala (Quezaltenango and San Marcos)

..... *B. purpusii* Brandegee

4. Uppermost internodes and elevated primary nerves on lower leaf surfaces densely covered with appressed brown hairs 1–2.5 mm long; pedicels 12–20 mm long; outer floral bracts 7–8 mm long; western Panama (Chiriquí) *B. gregii* Almeda

Among the green-flowered species, *B. gregii* is probably most closely related to *B. chlorantha*. They are separable even in sterile condition because *B. gregii* lacks the flap-like saccate pouches at the petiole-laminar junction that are typical of *B. chlorantha*. The latter also differs consistently in a number of other characters. Pubescence of the upper cauline internodes consists of ± flattened subulate hairs mostly less than 0.5 mm long and the floral bracts are beset with a mixture of spreading shaggy hairs (these mostly

less than 0.5 mm long) and appressed stellate hairs. In addition, the pedicels of *B. chlorantha* are shorter (0.4–1 cm), the calyx lobes are triangular instead of bluntly rounded, and the petals are about half the size ($6\text{--}8.5 \times 5\text{--}6$ mm) of those in *B. gregii*.

This species is named for Greg de Nevers (1955–), a student of Arecaceae, who collected the type and many other important additions to the melastome flora of Mesoamerica in the course of his extended field work in Panama from 1984 to 1986.

***Blakea hammelii* Almeda, sp. nov.**

(Fig. 6)

TYPE.—PANAMA. Chiriquí: 3.5 mi. NE of Boquete, end of rd. on slope S of Río Palo Alto, 17 Nov. 1978, *Hammel 5688* (holotype: CAS!; isotype: MO).

Frutex epiphyticus vel terrestris. Petioli 0.7–1.7 cm longi; lamina $3.5\text{--}7.5 \times 1.6\text{--}4.5$ cm elliptica vel elliptico-ovata apice caudata vel cuspidata basi acuta ad maturitatem subcoriacea et glabra, 5-nervata, nervi in axillis acarodomatii instructi, nervis secundariis 0.25 mm inter se distantibus. Flores 6-meri in quoque nodo superiore singuli vel bini, pedicellis 2.6–3.5 cm longis, bracteae omnino liberae; bracteae exteriores $3.5\text{--}5 \times 2\text{--}3$ mm ovatae vel ovato-ellipticae extus sparse subamorpho-furfuraceae demum glabrae; bracteae interiores $3\text{--}4 \times 3\text{--}3.5$ mm oblongo-ovatae extus sparse inconspicueque fimbriolato-ciliolatae. Hypanthium (ad torum) 3–4 mm longum extus glabrum; calycis tubus 1–1.5 mm longus, lobis $1\text{--}1.5 \times 2.5\text{--}3.5$ mm. Petala glabra $1.4\text{--}1.5 \times 0.8\text{--}0.9$ cm obovata apice rotundato. Filamenta 4.5–5.5 mm longa; antherae $3.5\text{--}4 \times 1\text{--}1.5$ mm oblongae lateraliter non cohaerentes apicaliter biporosae; connectivum dorsaliter ca. 1–1.5 mm supra thecarum basim tuberculatum. Stylus 10–11 mm; ovarium 5–6-loculare et $\frac{2}{3}$ inferum, cono glabro (collo non evoluto).

Epiphytic or terrestrial shrubs or small trees 2.5–6 m tall. Young vegetative buds deciduously furfuraceous, otherwise glabrous, the distal branchlets glabrous and bluntly quadrate with thickened interpetiolar lines or ridges. Mature leaves of a pair equal to unequal in size, glabrous throughout; petioles 0.7–1.7 cm long; blades subcoriaceous, $3.5\text{--}7.5$ cm long and $1.6\text{--}4.5$ cm wide, elliptic to elliptic-ovate, apex caudate to cuspidate, base acute, margin entire, 5-nerved abaxially with well-developed, irregularly ruptured domatia formed in the angles between the median vein and each of the two proximal lateral veins, the striolate transverse secondary veins spaced mostly less than 0.25 mm apart at the widest portion of the blade. Flowers erect, solitary or paired in leaf axils of distal branches; pedicels 2.6–3.5 cm long, glabrous. Floral bracts

sessile, entire, and free to the base; outer bracts $3.5\text{--}5 \times 2\text{--}3$ mm, ovate to ovate-lanceolate or elliptic-ovate, apex bluntly acute to rounded, sparingly and deciduously brown furfuraceous-puberulent; inner bracts $3\text{--}4 \times 3\text{--}3.5$ mm, oblong-ovate, apex rounded, essentially glabrous but deciduously fimbriolate-puberulent on the margins. Hypanthia (at anthesis) campanulate, 3–4 mm long to the torus and 6–7 mm in diameter, glabrous. Calyx tube 1–1.5 mm long; calyx lobes 1–1.5 mm long and 2.5–3.5 mm wide basally, broadly ovate with a blunt callose-thickened tooth at the abaxial apex of each lobe, margin entire, glabrous on both surfaces. Petals 6, glabrous, $1.4\text{--}1.5 \times 0.8\text{--}0.9$ cm, white flushed with pink unilaterally on the abaxial surface, obovate, apically rounded, entire. Stamens 12, isomorphic, free and declined to one side of the flower opposing the style; filaments complanate and glabrous, 4.5–5.5 mm long; anthers $3.5\text{--}4$ mm long, 1–1.5 mm wide, yellow, linear-oblong in dorsal and ventral view, narrowly ovoid in profile view, truncate at the apex with two somewhat dorsally inclined pores; connective slightly thickened dorsally and dilated into a blunt spur ca. 1–1.5 mm above the filament insertion. Ovary $\frac{2}{3}$ inferior, 5–6-celled, glabrous at the summit which is distended into a prominent cone that becomes rounded with age. Style declinate and somewhat sigmoid, glabrous, 10–11 mm long; stigma truncate. Berry globose, 5–6.5 mm long and 4–7 mm in diameter. Seeds irregularly pyriform to pyramidal, 0.5–1 mm long, beige with a smooth testa and conspicuous lateral raphe.

PHENOLOGY.—Flowering specimens have been collected from January through April and in November; the only known fruiting specimens were collected in January and April.

DISTRIBUTION.—Local and uncommon in cloud forests on the slopes of Cerro Pate Macho and along the Río Palo Alto in Chiriquí Province, Panama at 1,600–1,900 m (Fig. 8).

ADDITIONAL SPECIMENS EXAMINED.—PANAMA. Chiriquí: S slopes of Cerro Pate Macho, along trail E of Jaramillo Arriba, $8^{\circ}49'N$, $82^{\circ}23'W$, 12 Apr. 1984, *Churchill & Kuijt 5103* (CAS); trail to Cerro Pate Macho, $8^{\circ}49'N$, $82^{\circ}24'W$, 17 Jan. 1986, *de Nevers & McPherson 6830* (CAS); back side of mountain, Boquete, 20 Mar. 1977, *Folsom 2185* (CAS); along trail between N fork of Río Palo Alto and Cerro Pate Macho, ca. 6 km NE of Boquete, $8^{\circ}48'N$, $82^{\circ}23.5'W$, 6 Feb. 1986, *Grayum et al. 6371* (CAS); road along Río Palo Alto ca. 3 km NE of Boquete to the end, 15 Apr. 1982, *Huft 1855* (CAS); Río Palo Alto, 28 Apr. 1983, *Schmalzel 1478* (CAS).

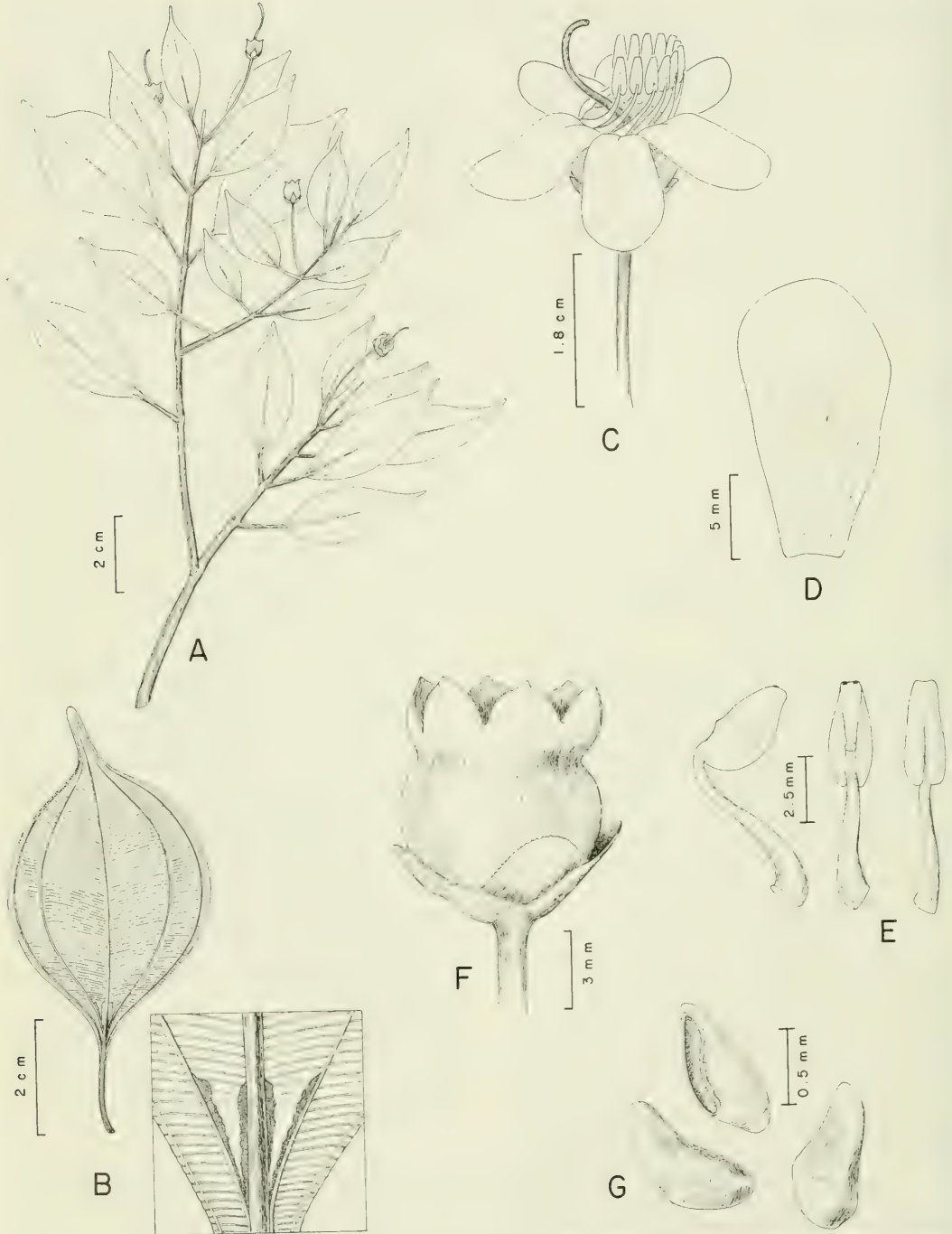


FIGURE 6. *Blakea hammelii* Almeda. A, habit; B, representative leaf with enlargement showing domatium (abaxial surface); C, representative flower (natural posture); D, petal (adaxial surface); E, stamens, lateral view (left), dorsal view (middle), ventral view (right); F, berry with persistent decussate bracts; G, seeds. (A, D, E from Churchill & Kuijt 5103; B from Huft 1855; C from de Nevers & McPherson 6830; F, G from Schmalzel 1478.)

Because of its elliptic to elliptic-ovate leaves with finely striolate secondary veins, erect long-pedicellate flowers, and white petals that are flushed with pink abaxially, *B. hammelii* is readily mistaken for *B. pauciflora* Gleason, to which it seems most closely related. The two differ primarily in androecial details and the nature of the calyx. In *B. pauciflora* the anthers, which are fused laterally for most of their length, are conic to rounded apically with two minute subterminal pores positioned on the ventral side of the anther sacs. Many specimens of *B. pauciflora* and *B. hammelii* are collected only in fruiting condition, but the flaring, essentially truncate, calyx of the former provides a consistent character by which the two species can be distinguished.

Although the domatia of *B. hammelii* and *B. pauciflora* are superficially similar to the pocket domatia of *Clidemia hammelii* Almeda (Almeda 1989), they appear to be modified versions of the pit or marsupiform (pocket-shaped) domatia described and illustrated by Jacobs (1966) and Stace (1965), respectively. The term domatium was coined by Lundström (1887) when he hypothesized a mutualistic relationship between mites and plants bearing these structures. Because of insufficient field study and the lack of experimental data, the functional significance of foliar domatia has remained conjectural for over a century. Based in part on Lundström's seminal paper, Pemberton and Turner (1989) recently presented new data to "support the hypothesis of a widespread facultative mutualism in which leaf domatia serve as shelters and nurseries for beneficial mites, which in turn reduce the number of phytophagous arthropods and pathogens using the plants." Interestingly, Pemberton and Turner found three genera of predaceous mites in 32% of the domatia of an unidentified Panamanian species of *Blakea* examined specifically for their study.

This species is named for Barry E. Hammel (1946–), avid student of the Mesoamerican flora, who collected the type of this and several other recently described species of Melastomataceae.

***Blakea herrerae* Almeda, sp. nov.**

(Fig. 7)

TYPE.—PANAMA. Comarca de San Blas: El Llano-Cartí road at about km 19. Ina Igar trail in the vicinity of Nusagandi, elev. 350 m, 1 Feb. 1989, Almeda et al. 6507 (holotype: CAS!; isotypes: AAU!, BM!, BR!, CR!, DUKE!, F!, G!, MA!, MEXU!, MICH!, MO!, NY!, P!, PMA!, TEX!, US!, WIS!).

Frutex epiphyticus. Ramuli subquadrangulares demum teretes primum sicut folia novella obscure furfuracei mox glabrati. Petioli 1–2 cm longi; lamina 6.5–11 × 3.2–5.8 cm elliptica vel elliptico-obovata apice caudata vel cuspidata basi acuta, 3-nervata vel 3-plinervata, subcoriacea et integra, nervis secundariis 0.25 mm inter se distantibus. Flores 6-meri in quoque nodo superiore 1–2(–3), pedicellis 0.5–1.2 cm longis, bractea omnino liberae; bractea exteriores 2.5–5 × 1.5–2.5 mm oblongo-lanceolatae acutae primum extus sparse vel modice subamorpho-furfuraceae demum glabratae; bractea interiores 2–4 × 2–3 mm ellipticae vel ovato-ellipticae apice late acuto extus glabrae. Hypanthium (ad torum) 3–4 mm longum extus sparsiuscule caduceque subamorpho-furfuraceum; calycis tubus 1.5–2.5 mm longus, lobis 1–2 mm longis. Petala 6–7 × 3–5 mm obovato-oblonga apice rotundato. Filamenta 3–4 mm longa; antherae 2.5–3 × 0.75–1 mm oblongae inter se lateraliter cohaerentes subapicaliter minute biporosae; connectivum nec prolongatum nec appendiculatum. Stylus 6–7 mm; ovarium 6-loculare et omnino inferum apice glabro (cono et collo non evoluto).

Epiphytic shrubs 2–4 m tall. Distal branchlets subquadrate, becoming rounded with age. Vegetative buds and very young leaves deciduously scurfy-puberulent. Mature leaves of a pair equal to somewhat unequal in size, glabrous throughout; petioles 1–2 cm long; blades subcoriaceous, 6.5–11 cm long and 3.2–5.8 cm wide, elliptic to elliptic-obovate, apex caudate to cuspidate or rarely varying to acuminate, base acute, margin entire, 3-nerved or 3-plinerved with an additional submarginal pair of inconspicuous veins, the striolate transverse secondary veins spaced mostly 0.25 mm apart at the widest portion of the blade. Flowers erect, solitary or paired, rarely in fascicles of three in each leaf axil of the distal branches; pedicels 0.5–1.2 cm long, sparingly scurfy-puberulent to glabrous. Floral bracts sessile, entire, and free to the base; outer bracts 2.5–5 × 1.5–2.5 mm, oblong-lanceolate, apex acute, sparingly to moderately scurfy-puberulent to glabrate; inner bracts 2–4 × 2–3 mm, elliptic to elliptic-ovate, apex acute, essentially glabrous but fimbriolate-puberulent on the margins. Hypanthia (at anthesis) campanulate, 3–4 mm long to the torus and 3–4 mm in diameter, sparingly and deciduously scurfy-puberulent. Calyx tube 1.5–2.5 mm long; calyx lobes 1–2 mm long and 2.5–3 mm wide basally, triangular to triangular-ovate, margin entire or deciduously ciliate, glabrous on both surfaces. Petals 6, glabrous, 6–7 × 3–5 mm, pale greenish-white, oblong-obovate, apically rounded, entire. Stamens 12, isomorphic; filaments 3–4 mm long, complanate, glabrous and declined to one side of the flower opposing the style; anthers 2.5–3 mm long, 0.75–1 mm wide, yellow, laterally connate for their entire length,

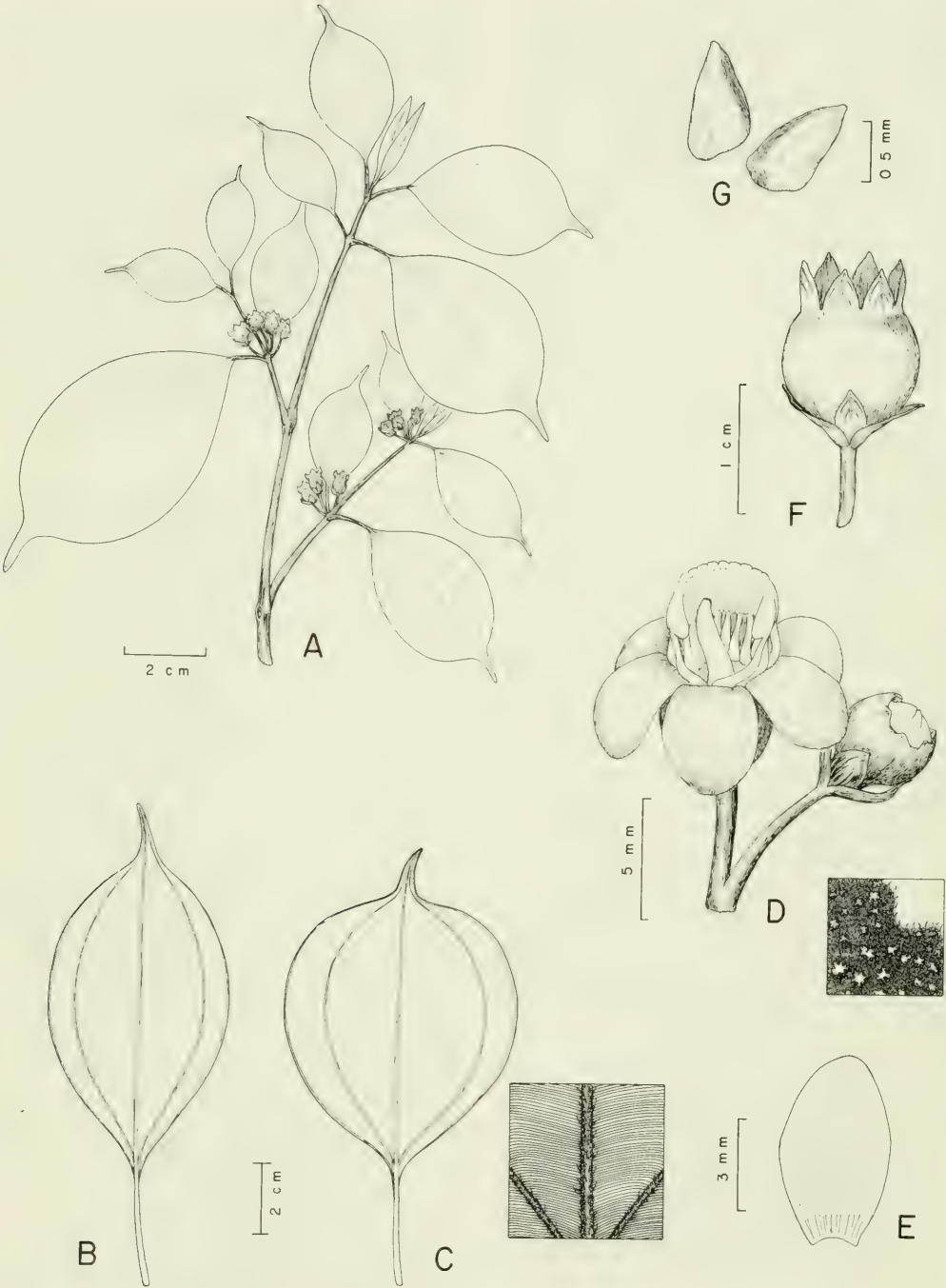


FIGURE 7. *Blakea herrerae* Almeda. A, habit; B, C, representative leaves (abaxial surface) showing variation in shape and enlargement (Coclé population) showing pubescence details; D, representative flower and bud (natural posture) with enlargement showing hypanthial pubescence; E, petal (adaxial surface); F, berry with persistent decussate bracts; G, seeds. (A-E from the holotype; F, G from Sytsma *et al.* 2603.)

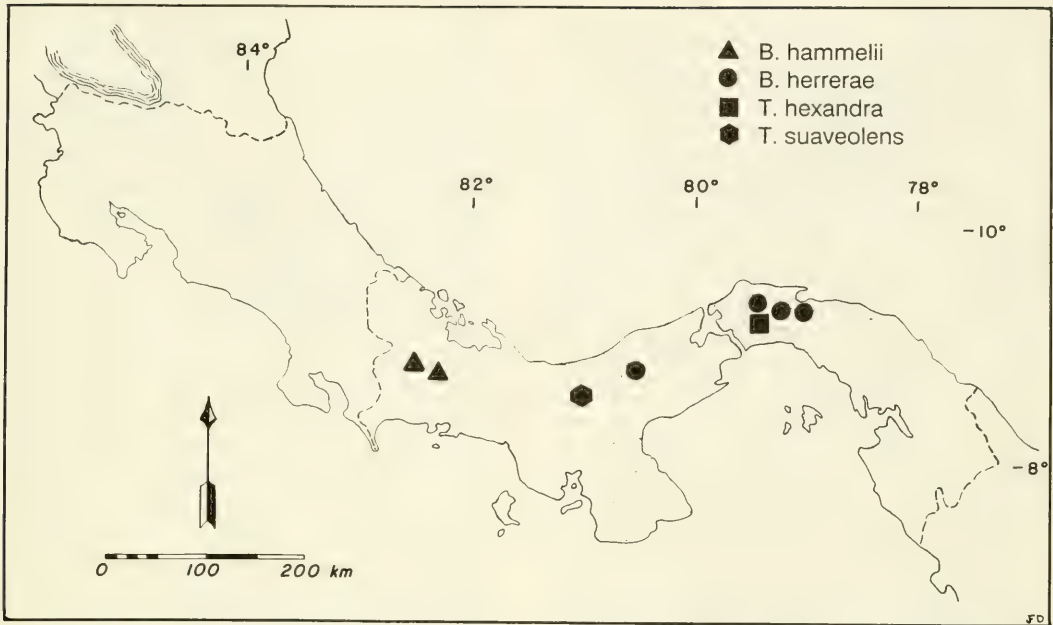


FIGURE 8. Distributions of *Blakea hammelii*, *B. herrerae*, *Topobea hexandra*, and *T. suaveolens*.

linear-oblong, with two minute pores positioned ventrally just below the truncate apex; connective slightly thickened dorsally but not prolonged or appendaged at the filament insertion. Ovary completely inferior, 6-celled, glabrous at the summit surrounding the stylar scar but not distended into a prominent cone or collar. Style somewhat declinate and slightly incurved distally, glabrous, 6–7 mm long; stigma truncate. Berry globose and pink at maturity, 9–10 mm long and 10–12 mm in diameter. Seeds clavate to narrowly pyriform or pyramidal, 1–1.5 mm long, beige with a smooth testa and conspicuous lateral raphe.

PHENOLOGY.—Flowering and fruiting occur sporadically throughout the year.

DISTRIBUTION.—Low rainforests from the Caribbean slope of central Panama (Coclé) east to the Llano-Cartí road in the Nusagandi region (Comarca de San Blas) at 100–400 m (Fig. 8).

ADDITIONAL SPECIMENS EXAMINED.—PANAMA. Coclé: between La Junta and Limón, 5 hr. walk N of Alto Calvario, 11 Oct. 1977, *Folsom 5878* (CAS); trail between Río Blanco and Continental Divide N of El Copé and El Petroso sawmill, 8°38'N, 80°36'W, 14 Dec. 1980, *Sytsma et al. 2603* (CAS). Comarca de San Blas: Llano-Cartí road, km 16, trail to creek on Atlantic drainage, 2 Feb. 1989, *Almeda et al. 6523* (CAS, PMA); Nusagandi, Llano-Cartí road, 28 Jul. 1984, *de Nevers & Todzia 3540* (CAS); along Llano-Cartí road, W of road 13.8

km to 15.8 km from Interamerican Hwy., 9°19'N, 78°55'W, 24 Aug. 1984, *de Nevers et al. 3746* (CAS); Llano-Cartí road, 13.8 km to 19 km from Interamerican Hwy., 9°19'N, 78°55'W, 3 Sep. 1984, *de Nevers & Porras 3822* (CAS); Llano-Cartí road, km 19.1, 9°19'N, 78°56'W, 9 Nov. 1984, *de Nevers & Herrera 4242* (CAS); Llano-Cartí road, km 19.1, 9°19'N, 78°55'W, 11 Mar. 1985, *de Nevers & Herrera 5100* (CAS). Comarca de San Blas/Panama Border: on Kuna divide trail N of Llano-Cartí road, 9°20'N, 79°00'W, 16 Dec. 1987, *McPherson 11879* (MO). Panama: Llano-Cartí road, 9°16'N, 78°58'W, 12 Sep. 1980, *Sytsma 1077* (CAS); headwaters of Río Chagres, Río Esperanza, and Río Piedras, 9°20'N, 79°20'W, 17 Oct. 1984, *de Nevers et al. 4088* (CAS).

First collected in 1977, *Blakea herrerae*, is another species that has been confused with, and is probably derived from, *B. pauciflora*. Both species have finely striolate secondary foliar venation and laterally fused anthers that are declined to one side of the flower to form a semicircle. *Blakea pauciflora* differs from *B. herrerae* in a number of floral characters. The pedicels of *B. pauciflora* are longer (2.5–5.3 cm), the calyx is essentially truncate and flaring, the style is longer (9–12 mm) and flexuous, and the larger petals (13–19 × 8–10 mm) are white flushed with pink instead of pale greenish-white. *Blakea herrerae* is also distinctive in that some mature leaves on all collections examined have cryptic tufts of short stiff hairs on the lower surface in the angles between the median vein and each of the two

proximal lateral veins. These may well function as acarodomatia, like the concentrated foliar hair tufts now known to harbor beneficial mites in many plant groups (Pemberton and Turner 1989).

There is some variation in the size and shape (Fig. 7B, C) of mature leaves, but none of this can be correlated with geography, elevation, or other diagnostic characters. Despite the limited range of this species, there is some variation that appears to be geographically correlated. The two cited collections from Coclé Province west of the Canal Area (Fig. 8) differ from populations east of the Canal in having elevated primary leaf veins below that are sparsely beset with a mixture of scurfy hairs and spreading glandular hairs. The lower leaf surfaces of these two collections are also unusual in having a liberal scattering of minute red glands on and between the striolate secondary veins. More material from Coclé and other intervening areas is needed to better assess the significance of these differences in pubescence.

A population from Cerro Jefe, Panama (represented by *D'Arcy 12181*, *McPherson 7435*, and *Sytzma 1414*, all CAS), is similar to *B. herrerae* in foliar venation, details of the floral bracts, and anther morphology. These collections differ from other cited material in having thicker leaves, larger petals (12–15 × 8–9 mm) that are pink, and longer styles (11–12 mm long). Because plants of this population differ from typical specimens of *Blakea herrerae* in characters that are commonly diagnostic, they are excluded from my circumscription of this species pending additional study.

Field study of this species in the Nusagandi region revealed an unusual method of vegetative reproduction that to my knowledge has never been reported for an epiphytic member of the Melastomataceae. *Blakea herrerae* is commonly a massive rainforest epiphyte with lax spreading branches that skirt host trees. In two individuals examined, the outermost branches were attached to adjacent trees by clinging adventitious roots. One individual had colonized four neighboring host trees in this fashion.

Blakea herrerae also appears to be unique among the erect-flowered species of the genus in having greenish-white flowers that produce a pleasant spicy fragrance but lack nectar. The fragrance is reminiscent of that produced by neotropical orchids that are pollinated by male euglossine bees. The few species of *Blakea* and *Topobea* with showy white and/or pink flowers

that have been studied in the field are buzz-pollinated by many species of bees (including two euglossine genera) seeking pollen as a floral reward (Lumer 1981; Renner 1989). Several euglossine genera are among the common buzz-pollinating bees in the neotropics (Buchmann 1983; Roubik 1989). However, only female euglossines are known to collect pollen from neotropical Melastomataceae (Renner 1989). In the male euglossine pollination syndrome of the Orchidaceae, the flowers produce no nectar and the pollen is not available as a food source. It will be interesting to learn if euglossine bees buzz-pollinate the poricidal anthers of *B. herrerae* and if its floral fragrance serves only as a secondary attractant, as suggested by Renner (1989) for melastomes in general. In addition to the Orchidaceae, floral fragrance collection by male euglossines has been found in some species of *Anthurium* and *Spathiphyllum* (both in the Araceae), one species of *Gloxinia* (Gesneriaceae), *Cyphomandra* (Solanaceae), *Dalechampia* (Euphorbiaceae), and a scattering of species in other families of flowering plants (Ackerman 1986; Williams 1983). Because pollen presentation in *Cyphomandra* provides a parallel to the poricidally dehiscent anthers of *Blakea herrerae*, additional fieldwork is needed to document details of its pollination biology.

This species is named for Heraclio Herrera (1959–), a student of the Panamanian flora who kindly directed me to a flowering population of this species at Nusagandi, Panamá.

***Blakea scarlatina* Almeda, sp. nov.**

(Fig. 9)

TYPE.—COSTA RICA. Alajuela: 20–30 km SE of Cataratas de San Ramón, elev. 2,150–2,500 ft. (655–762 m), 20 Mar. 1978, *Almeda et al.* 4308 (holotype: CAS!).

Frutex epiphyticus ca. 4 m altus. Ramuli primum subquad-rangulati demum teretes sicut folia novella pedicelli hypanthia-que sparse vel densi furfuracei demum glabrati. Petioli 1.7–4.5(–6.3) cm longi; lamina 8.5–19.7 × 5.4–10 cm elliptica vel elliptico-ovata apice acuminata basi acuta vel obtusa vel rotundata, 3-nervata, coriacea et integra, nervis secundariis 1–2 mm inter se distantibus. Flores 6-meri in quoque nodo superiore singuli, pedicellis 1–1.8 cm longis; bractee exteriores 2–2.7 × 2.2–3.6 cm late ovatae vel suborbiculares ca. 1–1.5 cm coalitae apice truncato-rotundato plerumque mucronato; bractee interiores 1–2 cm omnino coalitae. Hypanthium (ad torum) 1–1.3 cm longum; calycis tubus 5–6 mm longus, lobis 5–10 mm longis. Petala 3–4.5 × 2.5–4.3 cm obovata vel cuneata apice truncato vel rotundato. Filamenta 9–13 mm longa; antherae 6–8 × 4–6 mm inter se non cohaerentes, poris duobus minutis terminalibus; connectivum ad basim dorsaliter dente

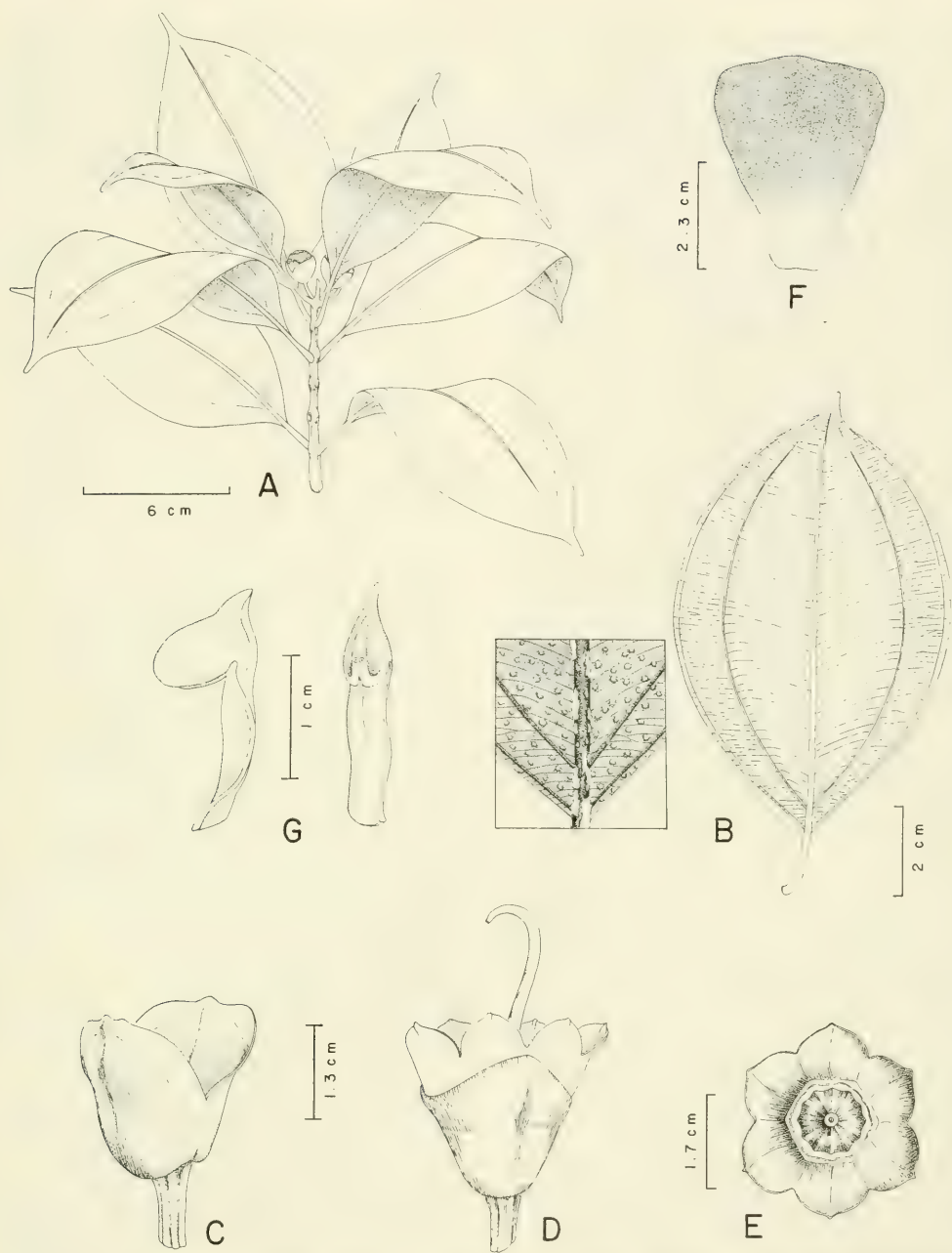


FIGURE 9. *Blakea scarlatina* Almeda. A, habit; B, representative leaf (abaxial surface) with enlargement showing pubescence detail; C, outer floral bracts; D, inner floral bracts enveloping hypanthium; E, hypanthium (top view) showing ovary summit, torus and calyx lobes; F, petal (adaxial surface); G, stamens, lateral view (left), ventral view (right). (A, B from the holotype; C–G from Hammel 9297, CAS.)

3–5 mm armatum. Stylus 2–2.1 cm; ovarium 6-loculare et omnino inferum cono 5 mm longo (collo incluso) glabro.

Massive epiphytic shrubs to 4 m tall with coarse spreading branches 0.5–8 m long. Vegetative

buds, juvenile leaves, pedicels, and young hypanthia sparsely to densely furfuraceous-puberulent but becoming glabrate with age. Mature leaves of a pair essentially equal or only slightly

unequal in size; petioles 1.7–4.5(–6.3) cm long; blades thick and coriaceous, 8.5–19.7 cm long and 5.4–10 cm wide, elliptic to elliptic-ovate, apex acuminate, base acute to obtuse or rounded, margin entire, 3-nerved with an additional pair of inconspicuous intramarginal veins, the transverse secondary veins mostly 1–2 mm apart at the widest portion of the blade, essentially glabrous but whitish punctulate above, sparsely furfuraceous-puberulent on the elevated primary veins below or almost glabrous. Flowers erect, solitary in the axils of uppermost leaves; pedicels somewhat compressed, 1–1.8 cm long. Floral bracts thick and coriaceous, sessile and entire; outer bracts connate basally for about half their length, $2\text{--}2.7 \times 2.2\text{--}3.6$ cm, broadly ovate to suborbicular, apex rounded to subtruncate, typically mucronate, deciduously furfuraceous-puberulent abaxially; inner bracts connate for their entire length to form a shallowly lobed, glabrous, bowl-like collar 1–2 cm high that envelops the hypanthium but is usually concealed by the outer bracts. Hypanthia (at anthesis) campanulate, 1–1.3 cm long to the torus and 1.3–1.6 cm in diameter. Calyx tube 5–6 mm long; calyx lobes erect or slightly spreading, 5–10 mm long and 9–14 mm wide basally, triangular-ovate and apiculate, margin entire, moderately to sparingly furfuraceous-puberulent abaxially. Petals 6, fleshy and glabrous when fresh, $3\text{--}4.5 \times 2.5\text{--}4.3$ cm, brilliant red but white for the basal $\frac{1}{4}$ of their length, obovate to cuneate, apically truncate to broadly rounded, entire. Stamens 12, isomorphic, free but connivent and forming a somewhat declinate nearly semicircular ring around the style; filaments complanate, white, fleshy and glabrous, 9–13 mm long; anthers 6–8 mm long and 4–6 mm wide, yellow, oblong-ovoid, laterally compressed and tipped with two minute pores; connective thickened and prolonged dorsally at the base into an acute spur 3–5 mm long that assumes a pseudoterminal position because of the pronounced adaxial tilt of each anther apex. Ovary completely inferior, 6-celled, glabrous at the gently fluted summit and dilated apically into a cone and stylar collar 5 mm long. Style declinate and incurved distally, glabrous, 2–2.1 cm long and 0.5–1 mm wide, stigma truncate to capitate. Mature berry and seeds not seen.

PHENOLOGY.—Flowering specimens have been collected in every month except December and January; of the nearly 40 collections available for this study none had mature fruits.

DISTRIBUTION.—Widespread but local and uncommon in wet evergreen forests from southern Nicaragua (Zelaya) south to Costa Rica from Parque Nacional Rincón de la Vieja (Guanacaste) and the Cordillera de Tilarán (Alajuela) south-east to the vicinity of Turrialba (Cartago) from sea level to 1,450 m (Fig. 5).

ADDITIONAL SPECIMENS EXAMINED.—COSTA RICA. Alajuela: 3 km N of Río Cataratas on road to Bajo Rodríguez, 23 Feb. 1978, *Almeda & Nakai 3884* (CAS, CR); 18–35 km NNW of San Ramón on road to Cataratas, 21 Mar. 1986, *Almeda et al. 5652* (CAS); La Palma de San Ramón, 6 Nov. 1923, *Brenes 3920* (F); La Palma de San Ramón, 29 Sep. 1925, *Brenes 4466* (F); La Palma de San Ramón, 24 Oct. 1926, *Brenes 5031* (F); La Palma de San Ramón, 24 Nov. 1926, *Brenes 5115* (F); La Palma de San Ramón, 24 Nov. 1926, *Brenes 5138* (F); La Palma de San Ramón, 22 Aug. 1927, *Brenes 5671* (F); La Palma de San Ramón, 5–8 Aug. 1935, *Brenes 20627* (F); Reserva Forestal de San Ramón above and in valley of Río San Lorencito, $10^{\circ}13'N$, $84^{\circ}37'W$, 12–14 Mar. 1987, *Burger et al. 12105* (CAS, F); Monteverde Reserve, Atlantic slope, Río Peñas Blancas valley, 19 Mar. 1986, *Haber 1519* (CAS); San Carlos, margin of Río Peñas Blancas at elevation of San Pedro, 29 Jun. 1985, *Haber & Bello 1744* (CAS); San Carlos, Peñas Blancas, 9 Jul. 1985, *Haber & Bello 1873* (CAS); Río Peñas Blancas, San Carlos, 11 Aug. 1985, *Haber & Bello 2306* (CAS); finca Don Bolívar Ruiz on road between the Reserva de San Ramón station and the road to Palmareña, Feb. 1987, *Herrera 508* (CAS); 6 km S of Ciudad Quesada, near Río La Vieja, 10 Sep. 1967, *Lent 1265* (F); 8 km NE of Villa Quesada, near Artezalea, 17 Feb. 1966, *Molina et al. 17258* (F); near San Isidro de Peñas Blancas, 22 Oct. 1965, *Schnell 231* (F); La Marina, near Ciudad Quesada, 23 Oct. 1965, *Schnell 243* (F); Villa Quesada, 21 Feb. 1939, *Smith H1603* (F); 5.8 km N of Cataratas de San Ramón, 11 Apr. 1976, *J. & K. Utley 4606* (CAS, DUKE). Cartago: Instituto Interamericano de Ciencias Agrícolas, Turrialba, 4 Oct. 1950, *León 2790* (MO); 2.5 km E of Tuis along banks of Río Tuis, 9 Mar. 1978, *Utley 6006* (CAS, DUKE). Cartago/San José Border: Estación Carrillo, Parque Nacional Braulio Carrillo, 28 Jul. 1984, *Zamora & Elizondo 672* (CAS). Guanacaste: Parque Nacional Rincón de la Vieja, Hacienda Santa María, SE of Mirador on road to Volcán Santa María, $10^{\circ}48'N$, $85^{\circ}19'W$, *Herrera & Robles 756* (CAS, MO). Heredia: Finca La Selva on Río Puerto Viejo, just E of its junction with the Río Sarapiquí, along Far Loop Trail, 1,000 m S, 21 Jul. 1980, *Hammel 9297* (CAS, DUKE, F); Finca La Selva on Río Puerto Viejo just E of its junction with Río Sarapiquí, ridge above Q. Esquina, 30 Aug. 1981, *Smith 135* (CAS, DUKE). Limón: hills 2 airline km SSE of Islas Buena Vista in Río Colorado, $10^{\circ}40'N$, $83^{\circ}40'W$, 13–14 Sep. 1986, *Davidse & Herrera 31127* (CAS); Hacienda Tapezco-Hda. La Suerte, 29 airline km W of Tortuguero, $10^{\circ}30'N$, $83^{\circ}47'W$, 28 Aug. 1979, *Davidson & Donahue 8913* (CAS); path beyond Río Sucio, Braulio Carrillo, May 1984, *Gomez et al. 22760* (CAS); ridge between Río Chirripó and Q. El Molinete, $10^{\circ}12'N$, $83^{\circ}54'W$, 19 Jul. 1984, *Grayum et al. 3553* (CAS); Cerro Coronel, E of Laguna Danto, $10^{\circ}41'N$, $83^{\circ}38'W$, 15–20 Sep. 1986, *Stevens & Montiel 24614* (CAS). Puntarenas: Monteverde community, windbreak next to road, $10^{\circ}20'N$, $84^{\circ}50'W$, 22 Jul. 1986, *Haber 5729* (CAS). NICARAGUA. Zelaya: 4 km N of Nueva Guinea, between Río Plata and San Antonio, $11^{\circ}44'N$, $84^{\circ}26'W$, 7 Sep. 1983, *Nee 27883* (CAS).

Blakea scarlatina is unique among its Central American congeners in having large flowers (8–9 cm across at anthesis) with brilliant red petals that are white for the basal $\frac{1}{4}$ of their length. For an obligate epiphyte this species has a comparatively broad geographic and elevational distribution; however, all available collections exhibit remarkable uniformity in floral and vegetative features.

Blakea scarlatina was first collected by A. M. Brenes in 1923. Many additional specimens have accumulated in herbaria since that time, but most have repeatedly been misidentified as *B. grandiflora* Hemsley. *Blakea grandiflora*, which is known only from higher elevations (1,400–2,350 m) in Costa Rica, differs in having 5-plinerved leaves with an additional intramarginal pair of veins, longer pedicels (3–5 cm), flowers borne in clusters of 2–4 in the upper leaf axils, petals that are white flushed with pink distally, and anther connectives that are modified dorso-basally into short deflexed spurs. Vegetatively, *B. scarlatina* has an aspect most reminiscent of *B. cuneata* Standley, a little-collected species of Belize, Guatemala, and Honduras. Striking similarities in foliar morphology and pubescence details initially led me to assign many collections of *B. scarlatina* to *B. cuneata*. Study of the type of *B. cuneata* and more recent collections, however, leaves no doubt that these two allopatric species are readily separated by a number of diagnostic characters. In *B. cuneata* there is a consistent tendency for the elliptic leaves to be narrower (3.5–6 cm), and the free portions of the outer floral bracts are elliptic-lanceolate and bluntly acute at the apex. *Blakea cuneata* also differs in having smaller petals (1.8–2.1 $\times$ 1.5–2 cm) that are pink, shorter filaments (5–6 mm), and linear-oblong anthers that are short (5–5.5 mm), erect, and unappendaged dorso-basally.

In anther morphology *B. scarlatina* most closely approaches *B. tuberculata* J. D. Smith and *B. cuatrecasii* Gleason. *Blakea tuberculata* also has anthers that are connivent and free, but they form a complete circle around the straight style. *Blakea cuatrecasii* has stamens that form a nearly circular ring opposing the declinate style, but the anthers are laterally fused for nearly half of their length. Because both of these species differ from *B. scarlatina* in so many other characters, I see no compelling reason to suggest that they form a particularly close alliance based solely on androecial morphology.

The flowers of *B. scarlatina* are some of the most spectacular among neotropical epiphytes. They are also some of the most enigmatic when attempting to make inferences about likely pollinators. The casual observer might be inclined to suggest bird pollination because of the brilliant red coloration of the petals. This seems highly unlikely. I have found no detectable nectar in any flowers examined in the field during morning and late afternoon hours. These observations are supported by Stein and Tobe (1989), who found no anatomical basis for nectar production in this species (referred to as *Blakea* sp. nov.).

Although pollinators of *B. scarlatina* remain unknown, a color slide photograph in the fragment packet of Burger *et al.* 12105 shows the brown anther discoloration (bruising) typically found on yellow-anthered melastome species that have been visited by buzz-pollinating bees. Field studies will be needed to determine the pollinator spectrum of this species and to evaluate conflicting reports on the nature of its floral fragrance. The flowers of *B. scarlatina* have been described as having a musky odor (Haber 1519), a distinct delicate fragrance (Almeda *et al.* 5652), and a strange, unpleasant odor (Nee 27883).

The name for this species is derived from *scarlatinus*, Latin for scarlet, in reference to the vivid red petal color.

***Topobea caliginosa* Almeda, nom. nov.**

Blakea micrantha Almeda, Rhodora 82:614. 1980.

TYPE.—PANAMA. Veraguas: Cerro Tute ca 10 km NW of Santa Fe on ridgetop in cloud forest above 1,000 m, 19 Jun. 1975, Mori 6765 (holotype: CAS!; isotype: MO!).

A study of anther morphology in recently collected flowering material of this species has led to the conclusion that it is closely related to *T. cordata*, *T. crassifolia*, and *T. hexandra*. This has necessitated a reassessment of the proper generic placement for this specialized group of species. For reasons discussed in the synoptic history at the beginning of this paper, it seems appropriate to transfer *Blakea micrantha* to *Topobea*. Adoption of a nomen novum is needed because the epithet *micrantha* is pre-empted in *Topobea* (Almeda 1981b:307). For additional comments and an enumeration of its diagnostic features, see the discussion under *T. hexandra*. The new name for this species is derived from *caligo*, Latin for fog, mist, or darkness, in reference to its fog-shrouded habitat at the summit of Cerro Tute.

***Topobea crassifolia* (Almeda) Almeda, comb. nov.**

Blakea crassifolia Almeda, *Rhodora* 82:612. 1980.

TYPE:—PANAMA. Coclé: La Mesa above El Valle in forest on both sides of junction with road to Cerro Pilón, ca 800 m, 21 Jul. 1974, *Croat* 25430 (holotype: CAS!; isotypes: MO!, US!).

The rationale for transferring *B. micrantha* to *Topobea* also applies to *B. crassifolia*. Among the four hexandrous species, *T. crassifolia* is most like *T. cordata* in having ovate to elliptic-ovate leaves and a 4-celled ovary. The leaves of *T. crassifolia* are petiolate whereas those of *T. cordata* are invariably sessile. Anther differences between these two species are discussed above under the synoptic history. With a distribution that extends to Costa Rica, *T. crassifolia* is the only hexandrous species known to occur outside of Panama.

***Topobea fragrantissima* Almeda, sp. nov.**

(Fig. 10)

TYPE:—PANAMA. Chiriquí: vicinity of Fortuna Dam, along trail across valley of Río Hornito, elev. 1,100–1,250 m, 12 Mar. 1988, *Almeda et al.* 6086 (holotype: CAS!; isotypes: CR!, F!, MO!, PMA!, TEX!, US!).

Frutex epiphyticus vel terrestris. Petioli 0.5–3 cm longi; lamina 1.5–5.5 × 1.6–3 cm elliptica vel elliptico-obovata apice acuminata basi acuta ad maturitatem glabra, 3-nervata vel 3-plinervata, subcoriacea et integra nervis secundariis 0.25 mm inter se distantibus. Flores 6-meri in quoque nodo superiore singuli vel bini, pedicellis 2–3 cm longis, bractaeae omnino liberae ellipticae vel obovatae; bractaeae exteriores 5–11 × 3–5 mm apice rotundato; bractaeae interiores 4–6 × 4–5 mm apice rotundato. Hypanthium (ad torum) 3–4 mm longum extus glabrum; calycis tubus 1 mm longus, lobis 1 mm longis. Petala 1.2–1.4 × 1–1.2 cm obovato-oblonga apice rotundato. Filamenta 5–6 mm longa; antherae 3.5–5 × 1 mm oblongae lateraliter non cohaerentes, poro unico dorsaliter inclinato; connectivum ad basim dorsaliter dente 0.25 mm longo descendenti armatum. Stylus 1–1.1 cm; ovarium 4-loculare et ½ inferum apice glabro (cono et collo non evoluto).

Epiphytic or terrestrial shrubs or small trees 1.5–4 m tall. Distal branchlets subquadrate and glabrous with interpetiolar ridges or lines. Vegetative buds and young leaves sparingly and deciduously lepidote-furfuraceous. Mature leaves of a pair equal to somewhat unequal in size, glabrous throughout; petioles 0.5–3 cm long; blades subcoriaceous, 1.5–5.5 cm long and 1.6–3 cm wide, elliptic to elliptic-obovate, apex acuminate, base acute, margin entire, 3-nerved or 3-plinerved abaxially with an additional submarginal pair of inconspicuous veins, the striolate transverse secondary veins spaced mostly 0.25

mm apart at the widest portion of the blade. Flowers erect, solitary or paired in leaf axils of distal branches; pedicels 2–3 cm long, glabrous. Floral bracts sessile, entire and free to the base; outer bracts 5–11 × 3–5 mm, elliptic or rarely varying to obovate, glabrous, apex rounded; inner bracts 4–6 × 4–5 mm, obovate, glabrous, apex broadly rounded. Hypanthia (at anthesis) campanulate, 3–4 mm long to the torus and 4–5 mm in diameter, glabrous. Calyx tube 1 mm long; calyx lobes 1 mm long and 1–1.5 mm wide basally, ovate to deltoid-ovate with a blunt callose-thickened tooth on the abaxial apex of each lobe, margin entire but sometimes roughened along interlobe sinuses, glabrous on both surfaces. Petals 6, glabrous, 1.2–1.4 × 1–1.2 cm, white flushed with pink unilaterally, obovate, apically rounded, entire. Stamens 12, isomorphic, free and strongly declined to one side of the flower opposing the style; filaments complanate and glabrous, 5–6 mm long; anthers 3.5–5 mm long, 1 mm wide, yellow, linear-oblong and tipped with a solitary dorsally inclined pore; connective dilated dorso-basally into a deflexed spur 0.25 mm long. Ovary ½ inferior, 4-celled, glabrous at the summit but not distended into a cone or collar. Style declinate and somewhat sigmoid, glabrous, 10–11 mm long; stigma punctiform. Berry globose, 7–10 mm long and 10 mm in diameter. Seeds clavate to narrowly pyriform or pyramidal, 1 mm long, beige with a smooth testa and conspicuous lateral raphe.

PHENOLOGY.—Flowering and fruiting specimens have been collected in January, March, April, and July.

DISTRIBUTION.—Local and uncommon in cloud forests from the Boquete region of western Panama (Chiriquí) to the slopes bordering the Río Hornito above Los Planes east to Cerro Colorado at 1,000–1,300 m (Fig. 5).

ADDITIONAL SPECIMENS EXAMINED.—PANAMA. Chiriquí: Edwin Fabrega Dam and Reserve along trail to Río Hornito above Los Planes, 8°45'N, 82°15'W, 18 Jan. 1989, *Almeda et al.* 6309 (CAS, MO, PMA); Monte Rey, above Boquete, 21 Jul. 1971, *Croat & Porter* 15692 (CAS, MO); trail to Zarzo, between Los Planes de Hornito and Fortuna Lake, 8°41'N, 82°13'W, *Hampshire & Whiteford* 689 (BM, CAS); ca. 5 km E of Fortuna Dam along trail crossing Río Hornito, 8°45'N, 82°15'W, 26 Apr. 1988, *Thompson* 5021 (CAS, CM). Chiriquí/Bocas del Toro Border: windswept cloud forest off the road to Cerro Colorado, 26 Jan. 1989, *Almeda et al.* 6418 (CAS, CR, DUKE, MO, PMA, US).

Topobea fragrantissima is distinguished by its glabrous leaves with finely striolate secondary

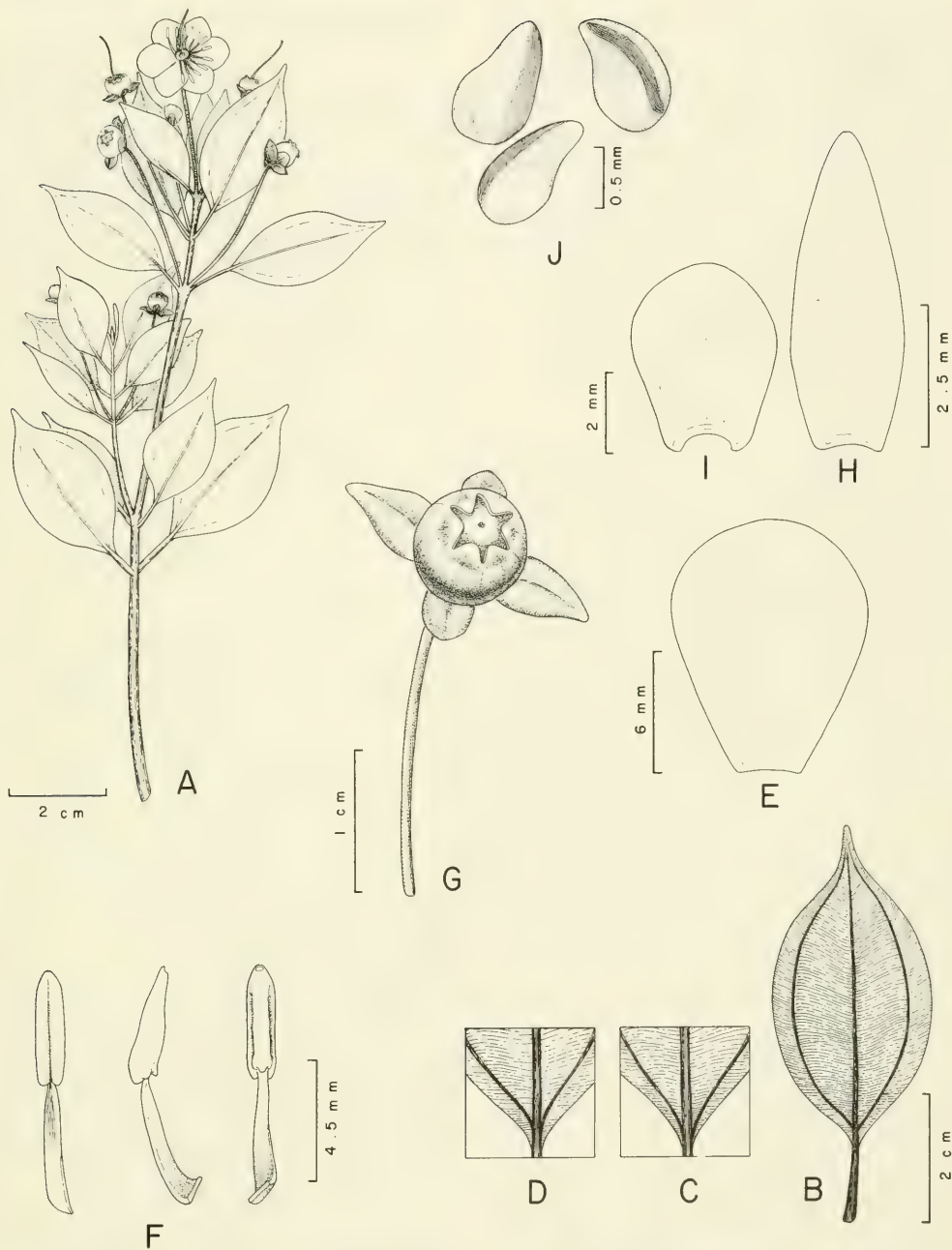


FIGURE 10. *Topobea fragrantissima* Almeda. A, habit; B, representative leaf (abaxial surface); C, D, enlargement of foliar venation (abaxial surface); E, petal (adaxial surface); F, stamens, ventral view (left), lateral view (middle), dorsal view (right); G, berry with persistent decussate bracts; H, outer floral bract (adaxial surface); I, inner floral bract (adaxial surface); J, seeds. (A–I from the holotype; J from Croat & Porter 15692, CAS.)

venation, long-pedicellate, erect flowers, linear-oblong anthers with solitary dorsally inclined pores, and a 4-celled ovary. Although it has been described as an epiphytic shrub or small tree, my

field observations and the label information on most collections suggest that this species typically becomes a small, free-living tree. The style in this species is declinate like many other species

of *Topobea*, but the posture and orientation of its androecium is unlike that of other congeners with free anthers. In the erect-flowered species of *Topobea* with free anthers, the filaments are declined to one side of the flower opposing the style and the anthers are typically erect or somewhat incurved apically. In *T. fragrantissima* this orientation is taken to such an extreme that both filaments and anthers lie flat on the surface of the petals to form a semicircular configuration (Fig. 10A). In this unusual androecial orientation the ventral surface of the anther faces upward and the dorsal surface (including the dorsally inclined pore) face downward toward the petal surface.

Field observations of pollination in this species should be of special interest because this pollen presentation mechanism is coupled with the production of a perfume-like fragrance. The unusual anther posture and orientation of the pore may require some peculiar manipulative behavior on the part of bees if this species is buzz-pollinated like the majority of species in the family with poricidally dehiscent anthers.

Topobea fragrantissima is similar to *T. suaveolens* (also described below) in a number of characters, and it seems likely that these two species are closely related. The shape and venation of mature leaf blades are nearly identical. In the few known collections of *T. suaveolens*, however, foliar pocket domatia (Fig. 12B) are formed abaxially in the angle between the median vein and the innermost pair of lateral veins; domatia are lacking in *T. fragrantissima*. The differences between these species are most readily apparent when fresh flowers are examined. In *T. suaveolens* the connivent petals give the pendant flowers a bell-like conformation, the free stamens form a ring around the straight style, and the ovary is 6-celled. The most distinctive feature shared by the two species is the solitary anther pore. Within the Blakeeae, this derived character is known in other species. *Topobea acuminata* Wurdack, *T. caudata* Wurdack, *T. dodsonorum* Wurdack, and *T. pittieri* Cogn. are a few notable examples. The fact that solitary anther pores occur in more than one species complex within *Topobea* suggests that this character has arisen more than once in the course of its evolutionary history.

The name for this species is derived from *fragro*, Latin for sweet smelling, in reference to the perfume-like fragrance of fresh flowers.

***Topobea hexandra* Almeda, sp. nov.**

(Fig. 11)

TYPE. — PANAMA. Panamá: Cerro Jefe, along summit road and along trail into the Chagres Valley, elev. ca. 900 m, 19 Feb. 1988, *Almeda et al.* 5837 (holotype: CAS!; isotypes: CR!, DUKE!, F!, MO!, NY!, PMA!, TEX!, US!).

Frutex hemiepiphyticus. Ramuli primum sulcato-quadrangulati demum teretes glabri (in nodis caduce puberuli pilis castaneis ca. 0.5–1 mm longis). Petioli 5–14 mm longi; lamina 2–3.9 × 1.1–3 cm subrotundata vel elliptico-ovata apice rotundato vel obtuso basi late acuta vel obtusa vel rotundata, 3-nervata coriacea et integra, nervis secundariis nervulisque invis. Flores 6-meri sessiles vel subsessiles in quoque nodo superiore singuli vel bini; bractae omnino liberae; bractae exteriores 5–6.5 × 3–5 mm ovatae vel ovato-ellipticae apice obtuso vel mucronato; bractae interiores 4–5 × 4–6 mm late ovatae vel suborbiculares apice rotundato. Hypanthium (ad torum) 3 mm longum extus sparsiuscule caduceque stellulato-furfuraceum; calycis tubus 1 mm longus, lobis 2 mm longis. Petala 6.5–7 × 4 mm obovato-elliptica apice obtuso. Filamenta 3 mm longa; antherae 6, ca. 2 × 1 mm oblongae inter se non cohaerentes, ventraliter biporosae; connectivum ad basim dorsaliter dente 0.25 mm descendenti armatum. Stylus 5.5 mm; ovarium 2-loculare et omnino inferum apice glabro (cono et collo non evoluto).

Hemiepiphytic shrubs to 1 m tall adhering to the bark of host trees by nodal and internodal adventitious roots. Distal branchlets quadrate to quadrisulcate, glabrous or sparsely beset with spreading, deciduous, glandular hairs 1–2 mm long like the young petioles and upper and lower surfaces of the juvenile leaves; older branches rounded with leaf scars that are typically swollen and nodular in appearance. Uppermost nodes copiously beset with brown spreading hairs. Vegetative buds copiously covered with a deciduous brown stellate-lepidote indument. Leaves of a pair equal in size, glabrous throughout; petioles 5–14 mm long; mature blades coriaceous, 2–3.9 cm long and 1.1–3 cm wide, suborbicular to elliptic-ovate, apex rounded or varying to obtuse, base obtuse to rounded, rarely varying to acute, margin entire, 3-nerved, often with an additional intramarginal pair of depressed veins. Flowers erect, solitary or paired in the leaf axils of distal branches, sessile or subsessile with short (to 1 mm) ill-defined pedicels formed by the compressed bases of the outer floral bracts. Floral bracts thick and semisucculent, sessile, entire and free to the base, sparingly stellulate-furfuraceous abaxially; outer bracts 5–6.5 × 3–5 mm, concave, ovate to elliptic-ovate, apex obtuse to bluntly mucronate; inner bracts 4–5 × 4–6 mm, broadly ovate to suborbicular, apex rounded. Hypanthia (at anthesis) narrowly campanulate,

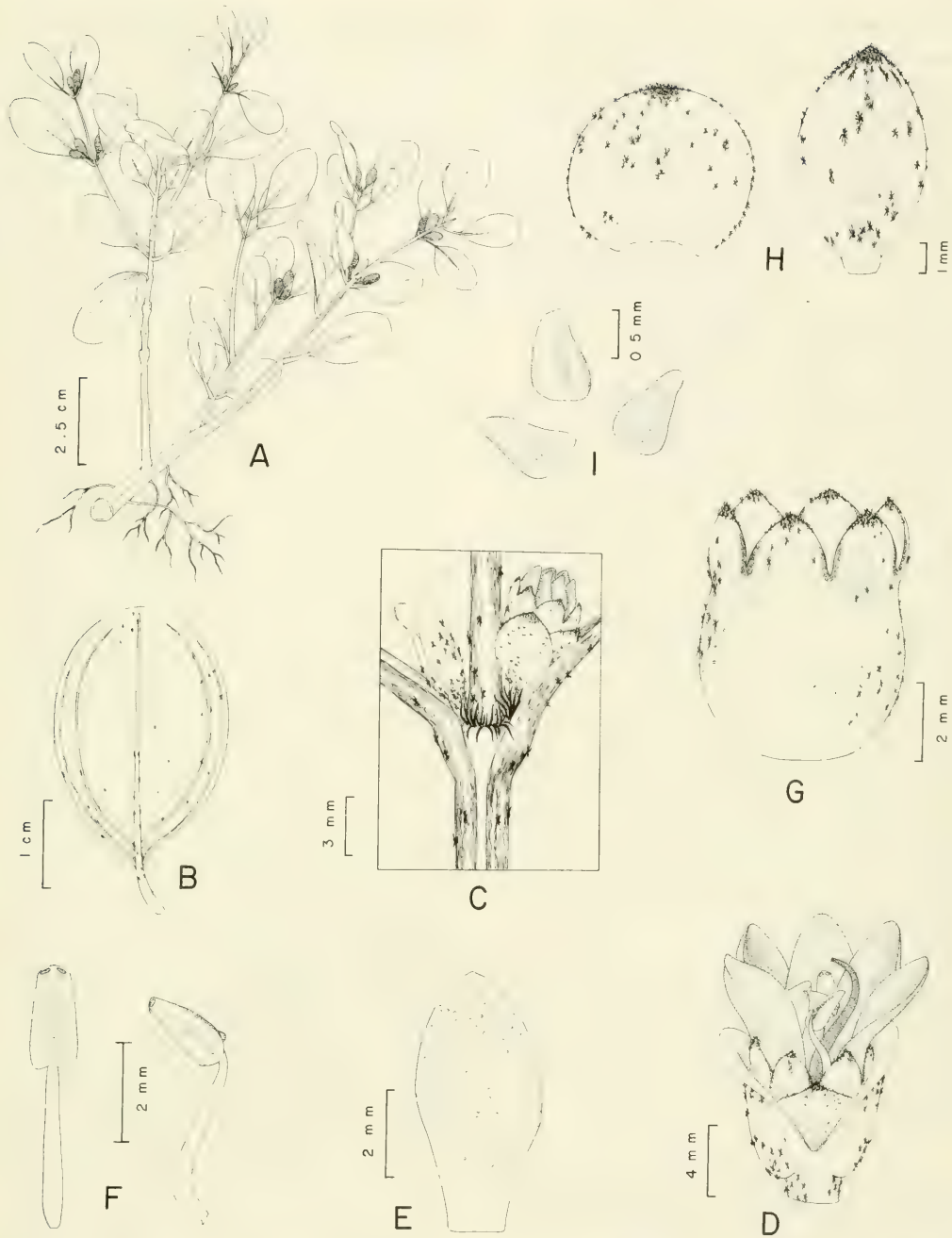


FIGURE 11. *Topobea hexandra* Almeda. A, habit; B, representative leaf (abaxial surface), C, enlargement of distal node showing spreading hairs; D, representative flower (natural posture); E, petal (abaxial surface); F, stamens, ventral view (left), lateral view (right); G, berry with persistent floral bracts removed; H, abaxial surface of inner floral bract (left), abaxial surface of outer floral bract (right); I, seeds. (A–H from the holotype; I from *Witherspoon* 8552.)

3 mm long to the torus and 4–5 mm in diameter, sparingly stellate-lepidote or stellulate-furfuraceous. Calyx tube 1 mm long; calyx lobes erect, 2 mm long and 2–2.5 mm wide basally, ovate to deltoid-ovate, entire but irregularly roughened along interlobe sinuses, sparingly stellate-lepidote. Petals 6, liberally covered with disc-shaped hyaline processes, 6.5–7 × 4 mm, pink, elliptic-obovate, apically obtuse, entire. Stamens 6, isomorphic and free; filaments complanate and glabrous, 3 mm long, declinate but incurved distally bringing the anthers to an incurved position opposing the style; anthers 2 mm long, 1 mm wide, pale yellow, turning brownish orange with age, oblong with two ventrally inclined pores at the broadly rounded apex; connective slightly thickened and dilated dorsally at the filament insertion into a short blunt spur up to 0.25 mm long. Ovary completely inferior, 2-celled, sparingly beset with stellate-lepidote hairs, glabrous at the summit surrounding the stylar scar but not distended into a prominent cone or collar. Style declinate, incurved distally, glabrous, 5.5 mm long; stigma punctiform. Berry globose, 5–6 mm long and 4–7.5 mm in diameter. Seeds bluntly deltoid, 1–1.5 mm long, beige with a smooth glossy testa and conspicuous lateral raphe.

PHENOLOGY.—The only known flowering specimens were collected in February; fruiting collections have been made in February, September, October, and December.

DISTRIBUTION.—Endemic to the low cloud forests on Cerro Jefe in central Panama at 900–1,000 m (Fig. 8).

ADDITIONAL SPECIMENS EXAMINED.—PANAMA. Panamá: summit and S facing slopes of Cerro Jefe, 9 Feb. 1978, *Almeda & Nakai 3459* (CAS); Cerro Jefe, along trail on ridge running NE from summit, 18 Dec. 1974, *Mori & Kallunki 3755* (MO); Cerro Jefe, 29 Oct. 1980, *Sytsma 2007* (MO); Cerro Jefe, road leading N from summit, 26 Sep. 1975, *J. T. & F. Witherspoon 8552* (MO).

Collections of *T. hexandra* are few despite the fact that it is one of the most common shrubby epiphytes in the forest at the summit of Cerro Jefe. In the field, fertile material is evidently overlooked without the aid of binoculars, because the small flowers are produced on uppermost branchlets positioned high on host trees where access to sunlight is optimal.

Topobea hexandra, together with *T. cordata*, *T. caliginosa* and *T. crassifolia*, form a closely related species group best interpreted as a spe-

cialized evolutionary line within the genus. They are distinguished from other congeners by a combination of specialized features associated with great reduction in flower size. These are: (1) flowers sessile or short-pedicellate (2–3 mm) at anthesis; (2) diminutive petals (4.5–9 × 1.5–6 mm); (3) each flower has only six stamens, each of which is attached to the torus opposite a calyx lobe; and (4) the ovary is 2-celled or 4-celled. The stamen number in *T. crassifolia* and *T. caliginosa* was unknown to me when I described these taxa, because all available study material had flowers with detached stamens (Almeda 1980). Recent collections of these two species and *T. cordata* clearly show that they are all hexandrous. The reduction in stamen number exhibited by this group of species is otherwise unknown in the tribe.

Among its close allies, *T. hexandra* is most similar to *T. caliginosa*. Both species have 3-nerved leaves, translucent petals that have a liberal scattering of hyaline disc-shaped gland-like processes, and 2-celled ovaries. *Topobea caliginosa* differs in having glabrous uppermost nodes, oblanceolate to spatulate, basally attenuate leaf blades, confluent anther pores, and unappendaged anther connectives.

Within its restricted range, *T. hexandra* shows inconstancy in characters of the indument. Distal branchlets can either be glabrous or sparsely beset with spreading glandular hairs. When present these hairs are found on distal internodes, petioles of juvenile foliage, and on upper and lower surfaces of some young leaves, but most of the hairs appear to fall away with age. All specimens of the type collection are devoid of glandular hairs. *Mori & Kallunki 3755* and *Witherspoon 8552* are beset with hairs as described above, but *Almeda & Nakai 3459*, which consists of two branches, has hairs on one branch but not on the other. Unfortunately, *T. hexandra* is known from too few collections to determine which, if any, of these forms constitutes the prevalent condition.

The epithet for this species is derived from the Greek words *hex*, six, and *andros*, male, in reference to the 6-stamened flowers.

***Topobea parvifolia* (Gleason) Almeda, comb. nov.**

Blakea parvifolia Gleason, *Phytologia* 3:357. 1950.

TYPE.—PANAMA. Coclé: crest of Cerro Pajita, El Valle de Antón, 1,100 m, *Allen 3761* (holotype: NY; isotype: MO!).

In the protologue, Gleason described the anthers of *Blakea parvifolia* as acute and emarginate at the tip with each anther sac opening by a separate dorso-terminal pore (Fig. 3B). Because anthers of this kind can only be interpreted as those of *Topobea*, Gleason appears to have erred in placing this species in *Blakea* and subsequently maintaining it in that genus for his treatment of the family in the Flora of Panama (Gleason 1958). Gleason's brief discussion in the protologue also stated that "the one flower remaining had lost part of its petals and stamens but there was no evidence that there had been more than four of the one and eight of the other." My study of this species in the field and herbarium shows that it has stamens that are coherent in a ring, as noted by Gleason, but the flowers are consistently 6-merous with 12 stamens.

Despite the heightened collecting activity in Panama during the past decade, *T. parvifolia* is still known only from the windswept slopes and ridges in the vicinity of El Valle de Antón.

***Topobea suaveolens* Almeda, sp. nov.**

(Fig. 12)

TYPE: PANAMA. Veraguas: along trail to summit of Cerro Tute about ½ mile above the Escuela de Agricultura Alto Piedra near Santa Fe, elev. 900–1,100 m, 29 Jan. 1989, *Almeda et al.* 6484 (holotype: CAS!; isotypes: AAU!, BM!, BRI!, CR!, DUKE!, FI, MEXU!, MICH!, MO!, NY!, PMA!, TEX!, US!).

Arbor epiphytica 4 m. Ramuli primum sulcato-quadrangulati demum teretes glabri; linea interpetiolaris paulo elevata evoluta. Petioli 1.1–1.8 cm longi; lamina 3.6–5.3 × 1.6–2.5 cm elliptica apice acuminata vel caudato-acuminata basi acuta, 3-plinervata, nervi in axillis acarodermatidis instructi, subcoriacea et integra, nervis secundariis 0.25 mm inter se distantibus. Flores 6-meri penduli in quoque nodo superiore singuli, pedicellis, 2.3–3 cm longis; bractae omnino liberae; bractae exteriores 4.5–7.5 × 3–4 mm ellipticae vel ovato-ellipticae apice acuto vel rotundato; bractae interiores 4–4.5 × 4 mm ovatae vel suborbiculares apice rotundato. Hypanthium (ad torum) 4 mm longum extus glabrum; calycis tubus 1.5 mm longus, lobis 1 mm longis. Petala 1.2–1.5 × 0.9–1.1 cm obovata apice rotundato. Filamenta 2.5–3.5 mm longa; antherae 2.5 × 1 mm oblongae inter se lateraliter non cohaerentes, poro unico dorsaliter inclinato; connectivum nec prolongatum nec appendiculatum. Stylus 8.5–9 mm; ovarium 6-loculare et ½ inferum apice glabro (cono et collo non evoluto).

Epiphytic trees to 4 m tall, often obscuring and overtaking the crowns of host trees. Distal branchlets quadrate to quadrisulcate and glabrous with well-defined interpetiolar ridges or lines. Vegetative buds deciduously lepidote-furfuraceous. Mature leaves of a pair equal or slightly unequal in size, glabrous throughout; petioles 1.1–1.8 cm long; blades subcoriaceous, 3.6–5.3

cm long and 1.6–2.5 cm wide, elliptic, apex acuminate to caudate-acuminate, base acute, margin entire, 3-plinerved with an additional inconspicuous pair of submarginal veins and numerous striolate transverse secondary veins spaced mostly 0.25 mm apart at the widest portion of the blade, pocket domatia typically formed abaxially in the angle between the median vein and the two proximal lateral veins. Flowers pendant and solitary in the leaf axils of uppermost branches; pedicels 2.3–3 cm long, glabrous. Floral bracts sessile, glabrous, entire, and free to the base; outer bracts 4.5–7.5 × 3–4 mm, elliptic to elliptic-ovate, apex bluntly acute to rounded; inner bracts 4–4.5 × 4 mm, ovate to suborbicular, apex broadly rounded. Hypanthia (at anthesis) campanulate, 4 mm long to the torus and 5.5–6 mm in diameter, glabrous. Calyx tube 1.5 mm long; calyx lobes 1 mm long and 4 mm wide basally, broadly ovate to deltoid-ovate with a blunt callose-thickened tooth on the abaxial apex of each lobe, margin entire, glabrous on both surfaces. Petals 6, glabrous, connivent to somewhat imbricate and bell-like when fully expanded, 1.2–1.5 × 0.9–1.1 cm, white flushed with dark pink along a broad continuous margin, ob-ovate, apically rounded, entire. Stamens 12, isomorphic, free and encircling the exerted style; filaments complanate and glabrous, 2.5–3.5 mm long; anthers 2.5 mm long, 1 mm wide, yellow, laterally compressed, oblong in ventral view and narrowly ovoid in profile view with a shallow dorso-basal depression at the filament insertion, tipped with a solitary, dorsally inclined pore 0.75 mm in diameter; connective simple. Ovary ½ inferior, 6-celled, dilated at the glabrous summit into a smooth gentle dome 1–1.5 mm high. Style straight, glabrous, 8.5–9 mm long; stigma truncate. Berry globose, 5–6 mm long and 6–7 mm in diameter. Seeds narrowly and irregularly pyriform, 0.75–1 mm long, pale brown with a smooth testa and prominent lateral raphe.

PHENOLOGY.—The three known collections of this species which are in flower and fruit were collected in January, February, and March.

DISTRIBUTION.—Known only from the cloud forests of Cerro Tute in west-central Panama at 850–1,100 m (Fig. 8).

ADDITIONAL SPECIMENS EXAMINED.—PANAMA. Veraguas: vicinity of Cerro Tute, along trail to summit, 08°30'N, 81°07'W, 19 Mar. 1987, *McPherson* 10654 (CAS); near Cerro Tute-Arizona, above Santa Fe and Alto de Piedra, 8°30'N, 81°10'W, 5 Feb. 1988, *McPherson* 12043 (CAS).

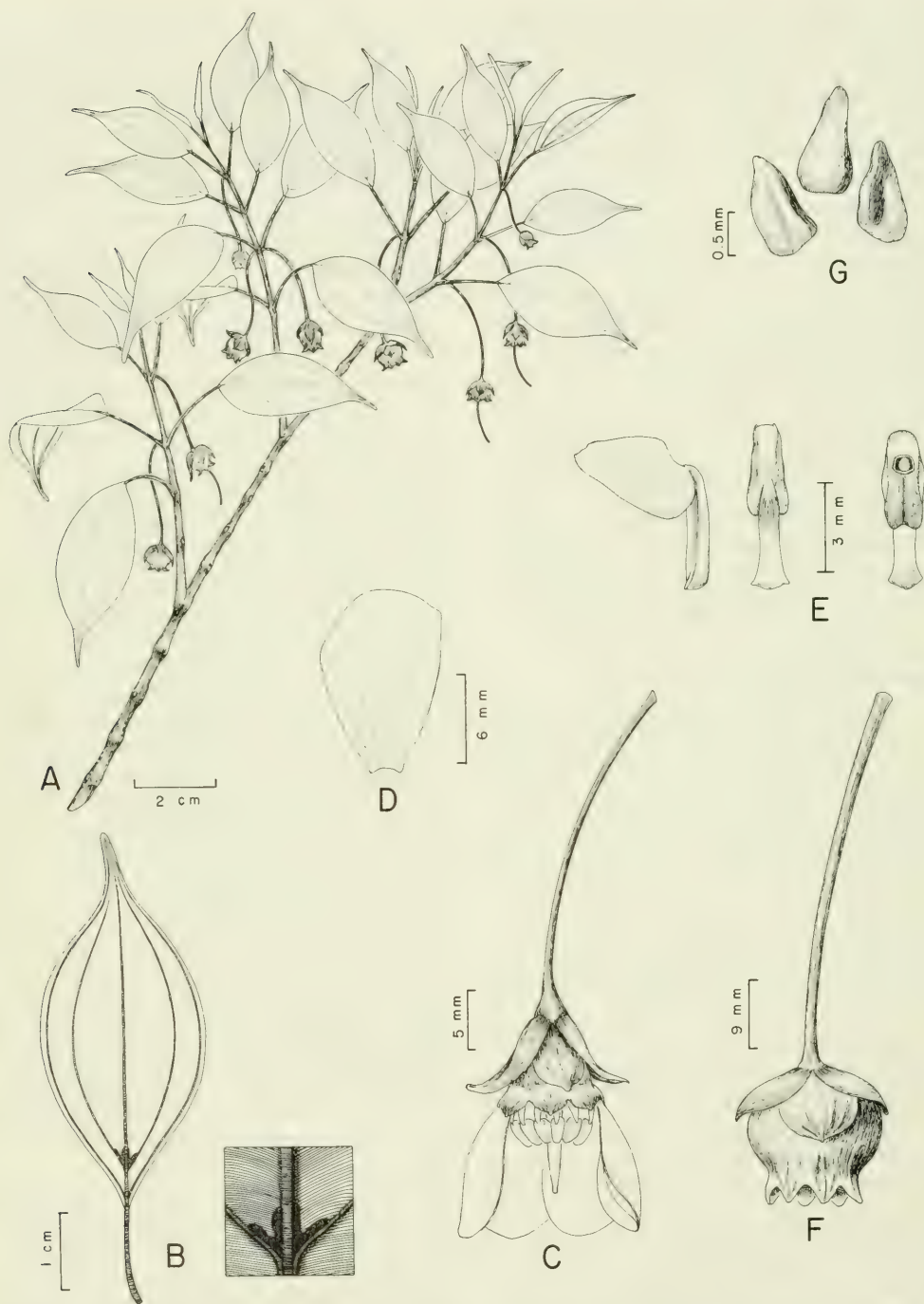


FIGURE 12. *Topobea suaveolens* Almeda. A, habit; B, representative leaf (abaxial surface) with enlargement showing domatium; C, flower (natural posture); D, petal (adaxial surface); E, stamens, lateral view (left), dorsal view (middle), ventral view (right); F, berry with persistent decussate bracts; G, seeds. (A-F from the holotype; G from McPherson 10654.)

Topobea suaveolens is unusual in having flowers that are bell-like and pendant with free connivent anthers that form a ring around the exerted straight style. This floral syndrome is not found in the other species of *Topobea* with brightly colored petals. *Topobea suaveolens* is clearly a sister species of *T. fragrantissima* (also described above). In addition to differences noted in the discussion of the latter, *T. suaveolens* is distinctive in at least two other floral features. Its filaments are conspicuously broadened at the base (Fig. 12E), and its shorter, laterally compressed anthers are narrowly ovate in profile view and have a conspicuous dorso-basal depression.

The strong vegetative similarities between *T. suaveolens* and *T. fragrantissima* can make identification of fruiting specimens difficult. Although *T. suaveolens* is known from few collections, even sterile material can be distinguished by the peculiar foliar pocket domatia that are formed abaxially in the angle between the midvein and the two proximal lateral veins (Fig. 12B).

Perhaps the most remarkable feature of this species is its agreeable floral fragrance. I described it as fruity (Almeda 6484), but a more telling comparison likens it to grape-flavored chewing gum (McPherson 12043). The name for this species is derived from *suavis*, Latin for sweet, in reference to the sweet-smelling flowers.

ACKNOWLEDGMENTS

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BM, BR, CM, CR, DUKE, F, K, MEXU, MO, NY, P, PMA, TEX, US, WIS.

RESUMEN

Blakea y *Topobea*, los únicos géneros en la tribu Blakeeae, están íntimamente relacionados, pero las anteras de *Topobea* tienen tecas lineal-oblongas, con uno o dos poros dorso-apicales o dos poros ventro-apicales. *Topobea* es un género con mas de 60 especies descritas, incluido en *Blakea* solamente por Don, Baillon y Macbride, pero es muy útil reconocerlo hasta que dispongamos de una monografía. Se presenta una historia taxonómica de los dos géneros con un comentario sobre las características de las anteras empleado originalmente por Browne, Aublet, Cogniaux, y otros botánicos. Las diferencias genéricas a menudo se han alterado un poco para reflejar mejor las características inusuales de algunas especies que se encuentran en las montañas de Costa Rica y Panamá. Se provee una clave nueva para los dos géneros. Se describen cuatro especies nuevas de *Blakea* (*B. gregii*, *B. hammelii*, y *B. herrerae* de Panamá; y *B. scarlatina* de Costa Rica y Nicaragua), y tres especies nuevas de *Topobea* (*T. fragrantissima*, *T. hexandra*, y *T. suaveolens* de Panamá) y se transfieren tres especies de *Blakea* a *Topobea*. Estos cambios se basan en características de las anteras. Se proveen descripciones, ilustraciones y discusiones sobre las afinidades entre las especies nuevas. Además se presentan notas sobre polinización y mapas de distribución.

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THREE NEW SPECIES OF *CONOSTEGIA*
(MELASTOMATACEAE: MICONIEAE) FROM
SOUTHERN CENTRAL AMERICA

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ABSTRACT: Three new species of *Conostegia*, a well-defined berry-fruited genus of Melastomataceae with a center of diversity in Costa Rica and Panama, have been collected in little-explored regions of southern Costa Rica and western Panama during the past decade. Descriptions, discussions, diagnostic illustrations, phenological notes, and a distribution map are provided for *Conostegia fragrantissima*, *C. muriculata*, and *C. orbeliana*. Attention is drawn to the need for recording field data on taxonomically useful floral and fruit characters.

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INTRODUCTION

Conostegia, a neotropical genus of about 50 species is one of approximately 30 berry-fruited genera assigned to the New World tribe Miconieae. Unlike some genera in this large tribe of 1,800-1,900 species, *Conostegia* is a natural assemblage readily defined by its terminal inflorescence, calyptriform calyx that is circumscissile at or near the torus, and isomorphic stamens with lorate anthers and unappendaged connectives. *Conostegia* is also noteworthy among neotropical Melastomataceae because most (but not all) of its species have flowers that are anisomerous and typically pleiostemonous. Among other genera in the Miconieae only a few species of *Clidemia* and *Miconia* have flowers with unequal numbers or proportions of serially homologous structures.

Variation in several species of *Conostegia* remains imperfectly understood because of inadequate geographic sampling and fragmentary preservation of floral characters on herbarium

specimens. Petal and stamen numbers, the posture and orientation of the style, stigma morphology, and ovary cell number provide useful information for the delimitation of species in *Conostegia*. These characters are often difficult to evaluate after specimens have been pressed and dried. Ideally, notes on these features should be recorded in the field when the preservation of flowers and fruits in a liquid medium is not feasible.

The three species described below all come from rich, but little-known, areas of Costa Rica and Panama. Over 33 species of *Conostegia* occur in this small isthmian region, making it the center of diversity for the genus and a promising area for continued botanical exploration in the Mesoamerican region.

Conostegia fragrantissima Almeda, sp. nov.

Fig. 1

TYPE.—PANAMA. Bocas del Toro. Fortuna Dam area, along continental divide trail bordering Chiriquí Province at 8°45'04"N, 82°15'04"W, 1,200-1,300 m, 10 Mar. 1988, Al-

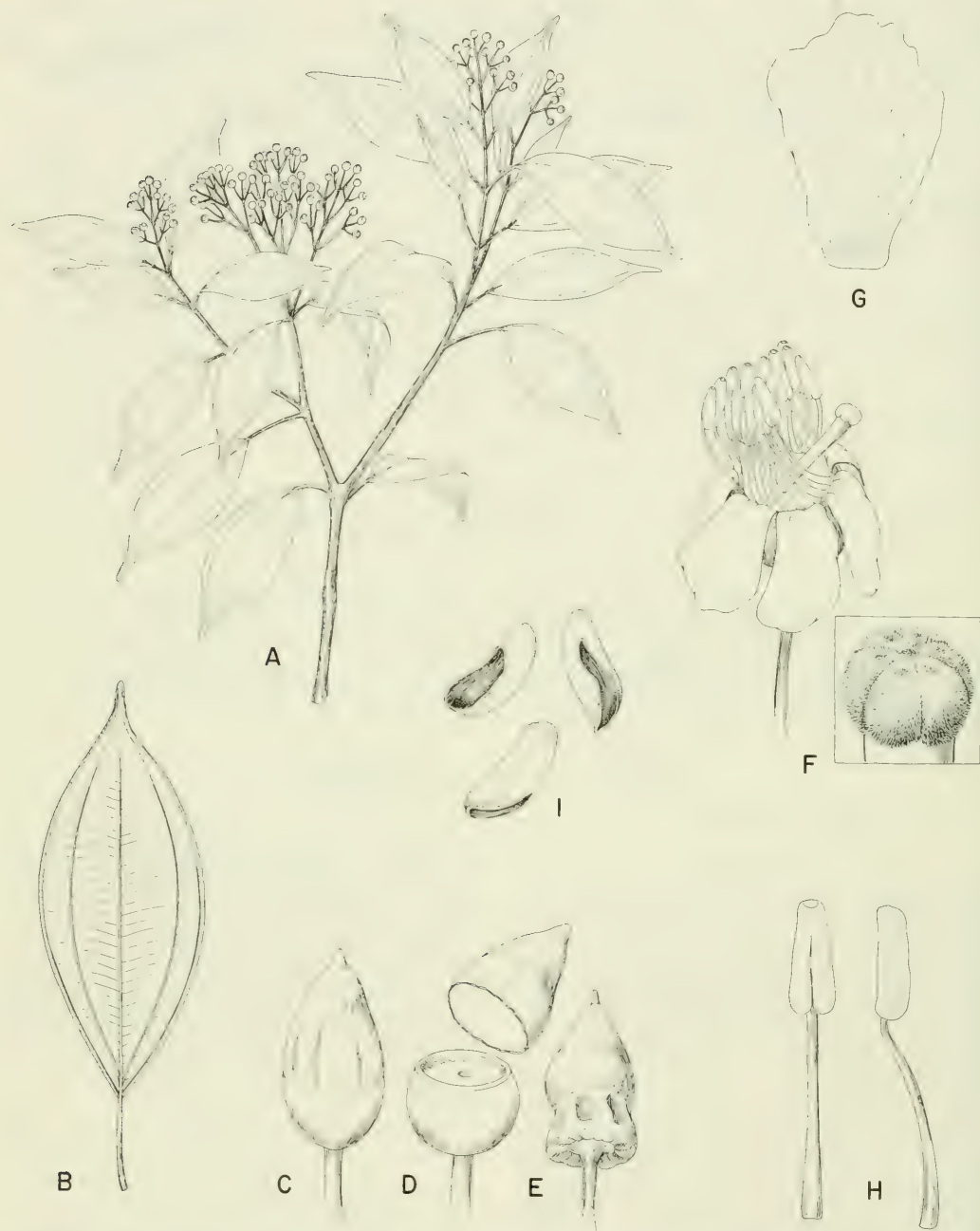


FIGURE 1. *Conostegia fragrantissima* Almeda. A, habit, $\times$ ca. $\frac{1}{5}$; B, representative leaf (abaxial surface), $\times$ 1; C, flower bud when fresh, $\times$ ca. 4; D, young berry with detached calyptriform calyx, $\times$ 5; E, flower bud when dry, $\times$ ca. 4; F, representative flower showing reflexed petals, declinate style and stigma enlargement (right), $\times$ ca. 3; G, petal (adaxial surface), $\times$ ca. 5; H, stamens, ventral view (left) and lateral view (right), $\times$ ca. 8; I, seeds, $\times$ ca. 30. (A-I from the holotype.)

meda et al. 6064 (holotype: CAS!; isotypes: AAU!, BM!, BR!, CR!, DUKE!, F!, MEXU!, MO!, NY!, PMA!, TEX!, US!).

Arbor 4–11 m. Ramuli primum quadrangulati demum teretes glabri; linea interpetiolaris paulo elevata evoluta. Petioli

1–2.6 cm longi; lamina 4.5–9.5 $\times$ 1.5–4.2 cm elliptica vel elliptico-lanceolata apice acuminata vel caudato-acuminata basi acuta, 3(–5)-plinervata, membranacea et integra supra glabra, subtus sparsiuscule caduceque lepidota. Inflorescentia 4–7.5 cm longa multiflora; pedicellis (ad anthesim) 2.5–7 mm longi;

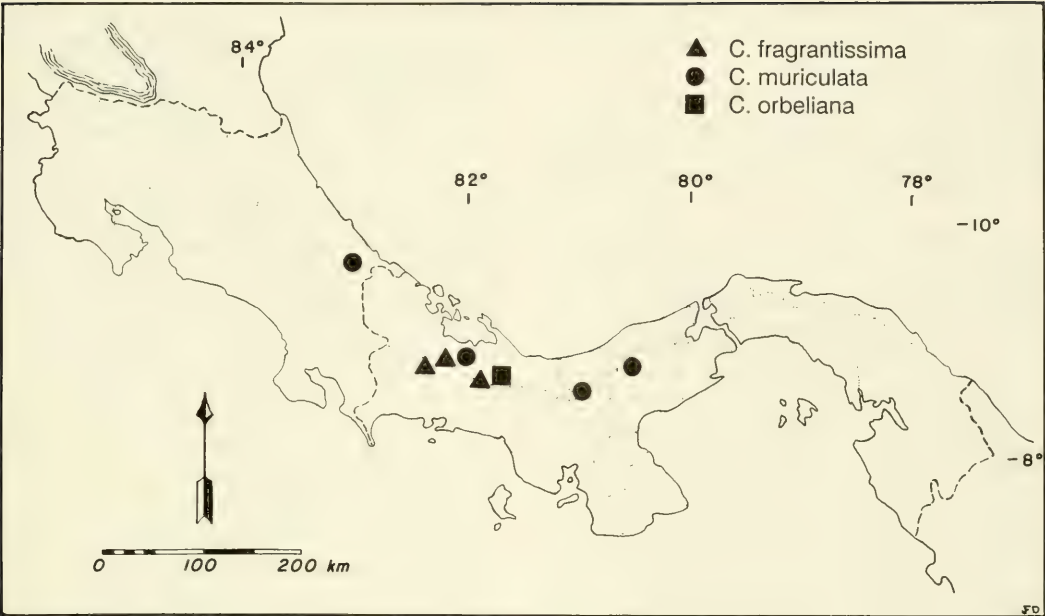


FIGURE 2. Distributions of *Conostegia fragrantissima*, *C. muriculata*, and *C. orbelliana*.

bracteolis 0.25–1.5 mm longis mox caducis. Alabastra matura acuminata vel apiculata 5–7 × 2–3 mm; calyx calyptriformis 3–4.5 mm longus. Petala 6–7, glabra 5–7 × 3.5–4.5 mm, obovata apice irregulariter rotundato. Stamina 15–19, isomorphica glabra; filamenta 2–2.5 mm longa; antherarum thecae 1.5–2 × 0.5 mm oblongae, poro ventraliter inclinato; connectivum nec prolongatum nec appendiculatum. Stylus 5–5.5 mm glaber; stigma capitatum 1.5 mm diam.; ovarium 6-loculare et omnino inferum apice glabro (cono et collo non evoluto).

Trees 4–11 m tall. The distal branchlets glabrous and bluntly quadrate with darkened interpetiolar lines or ridges. Leaves of a pair equal to somewhat unequal in size; petioles 1–2.6 cm long; blades membranaceous, 4.5–9.5 cm long and 1.5–4.2 cm wide, elliptic to elliptic-lanceolate, apex acuminate to caudate-acuminate, base acute, margin entire, 3(–5)-plinerved, the innermost pair of elevated primaries diverging from the median nerve in opposite fashion (1–)3–5 mm above the blade base, glabrous above, sparsely and deciduously furfuraceous-lepidote below. Inflorescence a terminal paniculiform dichasium 4–7.5 cm long typically branching above the node initiating the inflorescence, the rachis inconspicuously and deciduously furfuraceous-lepidote; bracteoles sessile to subsessile, early deciduous, narrowly triangular to subulate or linear-oblong, 0.25–1.5 mm long, 0.25 mm wide, glabrous, margin entire. Pedicels 2.5–7 mm long, decidu-

ously furfuraceous-lepidote. Flower buds oblong-ellipsoid, becoming horizontally constricted at the torus and truncate at the base when dry, 5–7 mm long, 2–3 mm wide, smooth and glabrous or sparsely furfuraceous-lepidote, the calyptriform calyx 3–4.5 mm long, acuminate to apiculate; torus glabrous adaxially. Petals 6–7, glabrous, white with a horizontal red band near the base, obovate, reflexed, irregularly lobed apically, 5–7 mm long and 3.5–4.5 mm wide distally. Stamens 15–19, gently declined to one side of the flower opposing the style; filaments glabrous, complanate, 2–2.5 mm long; anthers 1.5–2 mm long, 0.5 mm wide, orange, linear-oblong, truncate to broadly rounded at the apex with a somewhat ventrally inclined terminal pore 0.25 mm in diam.; connective thickened dorsally but not prolonged or appendaged at the filament insertion. Ovary (at anthesis) completely inferior, 6-celled, ovoid, the apex glabrous, smooth and lacking an elevated cone or collar. Style declinate, glabrous, 5–5.5 mm long; stigma capitate, 1.5 mm in diam. with 6–7 papillose lobes. Berry depressed-globose, 3 mm long and 4 mm in diam. Seeds oblong, oblong-ovoid, or narrowly pyramidal, 0.5–0.75 mm long, beige, smooth and polished on the convex face.

PHENOLOGY.—Flowering specimens have been

collected in the months of February through May; fruiting specimens have been collected in February and April.

DISTRIBUTION.—Local in wet evergreen and elfin forests of western Panama from Cerro Pate Macho (Chiriquí) to the Cerro Colorado region (Bocas del Toro) at 1,200–2,000 m (Fig. 2).

ADDITIONAL SPECIMENS EXAMINED.—PANAMA. Bocas del Toro: Fortuna Dam area, along continental divide trail, 8°45'04"N, 82°15'04"W, 10 Mar. 1988, *Almeda et al.* 6068 (CAS); Fortuna Dam region near trail along continental divide, 8°45'N, 82°15'W, 11 Feb. 1986, *McPherson* 8406 (CAS); vicinity of Cerro Colorado on trail along creek 8.6 miles from Camp Chamí, 8°35'N, 81°45'W, 14 Apr. 1986, *McPherson* 8900 (CAS); vicinity of Cerro Colorado mine above San Felix, 8°35'N, 8°50'W, 26 Jan. 1988, *McPherson* 12024 (CAS). Chiriquí: SE slopes and summit of Cerro Pate Macho, 4 km NE of Boquete, 26 May 1981, *Sytsma et al.* 4884 (CAS).

This species is distinguished by a combination of indument and floral characters. The lower leaf surfaces, branchlets of the inflorescence, pedicels, and distal cauline internodes are sparsely beset with deciduous furfuraceous-lepidote hairs. Although many specimens superficially appear glabrous to the unaided eye, the inconspicuous indument is readily detected on one or all of the above-mentioned structures when examined with a dissecting microscope. Aside from the declinate style and lobulate depressed-capitate stigma, most of the distinctive floral features are not readily gleaned from herbarium specimens without good field notes. The flowers are fragrant, the anthers are bright orange in color, and each conspicuously reflexed white petal has a red horizontal band near the base. This distinctive petal coloration is, to my knowledge, otherwise unknown in *Conostegia*.

The closest relative of *C. fragrantissima* is probably *C. pittieri* Cogn., a species known only from Costa Rica and Nicaragua. They both have elliptic to elliptic-lanceolate, caudate-acuminate, plinerved leaves and flowers with similar petal and stamen numbers. *Conostegia pittieri* is glabrous throughout, and its leaves are prevailing undulate-denticulate. It also differs from *C. fragrantissima* in having longer floral buds (9–13 mm), larger petals (9–13 × 5–8 mm), more ovary cells (8–10), and a crateriform capitate stigma.

In Gleason's treatment of *Conostegia* for the Flora of Panama (Gleason 1958), *C. fragrantissima* keys closest to *C. montana* (Sw.) D. Don ex DC., a widespread species ranging from southern Mexico (Chiapas) and the West Indies (How-

ard 1989) south through Central America to Colombia, Venezuela, and Ecuador. *Conostegia fragrantissima* shares many features with *C. montana* including foliar shape, petal and stamen numbers, and the number of ovary cells, but the latter has stellate hairs on the inflorescence rachis, pedicels, and elevated primary veins on lower leaf surfaces. In addition, the flowers of *C. montana* produce no detectable odor, the pedicels are shorter (1 mm), the petals are completely white, the anthers are pale yellow, and the style (when dry) is abruptly expanded just below the subtruncate unlobed stigma. The style and stigma enlargement of *C. fragrantissima* (Fig. 1F) was drawn from liquid-preserved flowers. Upon drying, the style retains its linear outline, but the capitate stigma becomes gently fluted and bluntly obconic in profile view.

The fragrant flowers of *C. fragrantissima* are unusual but not unique among its congeners. The flowers of *C. pittieri* are also fragrant (fide *Lumer* 1148, CAS), but information of this kind is rarely reported on herbarium labels. In choosing the epithet for this species, which is derived from *fragro*, Latin for sweet smelling, I draw attention to the very fruity fragrance of the fresh flowers.

Conostegia muriculata Almeda, sp. nov.

(Fig. 3)

TYPE.—PANAMA. Bocas del Toro: Above Chiriquí Grande, 10 road-miles from the continental divide and 2 miles along road to the east, 8°55'N, 82°10'W, 300 m, 6 Aug. 1988, *McPherson* 12836 (holotype: CAS!; isotypes: CR!, DUKE!, MO!, PMA!, US!).

Frutex vel arbor parva 2.5–3.5 m. Ramuli primum acute quadrangulati demum teretes glabri; linea interpetiolaris obscure evoluta. Petioli 1.5–7 cm longi; lamina 8–25.5 × 4.5–14 cm elliptica vel obovato-elliptica apice acuminata basi acuta, 5-nervata vel 5–7-plinervata, membranacea et integra, supra glabra, subtus sparsiuscule caduceque lepidota. Inflorescentia 12–30 cm longa (pedunculo 4–10 cm longo incluso) laxa multiflora; pedicellis (ad anthesim) 0.5–3 mm longis; bracteolis 0.5–1 mm longis mox caducis. Alabastra matura acuminata 6–10 × 3.5–4.5 mm; calyx calyptriformis 3–5 mm longus. Petala 5, glabra, 5–6 × 4–5(–6.5) mm, obovata apice rotundato. Stamina (8)–9–10, isomorphica glabra; filamenta 2.5–3 mm longa; antherarum thecae 2–3 × 0.75 mm oblongae, poro ventraliter inclinato; connectivum nec prolongatum nec appendiculatum. Stylus 3–4 mm glaber; stigma capitatum 0.75 mm diam.; ovarium 6-loculare et omnino inferum apice glabro (cono et collo non evoluto).

Shrubs or small trees 2.5–3.5 m tall. The distal branchlets glabrous with interpetiolar lines, quadrate and carinate on the angles but becom-

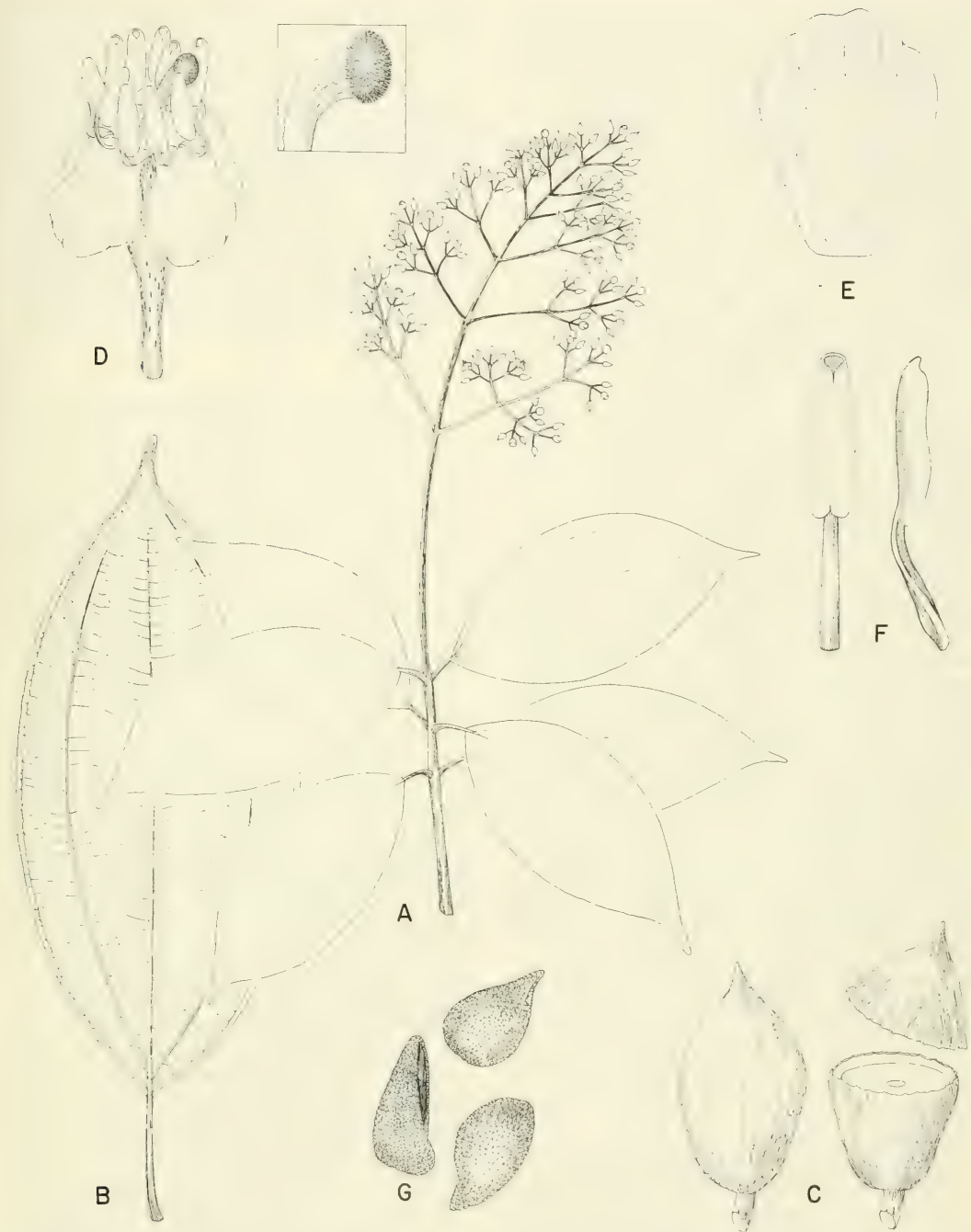


FIGURE 3. *Conostegia muriculata* Almeda. A, habit, $\times$ ca. $\frac{1}{4}$; B, representative leaf (abaxial surface), $\times$ $\frac{1}{2}$; C, flower bud (left) and bud with detached calyptriform calyx and floral parts removed (right), $\times$ 4; D, representative flower showing spreading petals, arching style, and stigma enlargement (right), $\times$ 5; E, petal (adaxial surface), $\times$ 6; F, stamens, ventral view (left) and lateral view (right), $\times$ 7; G, seeds, $\times$ 26. (A–F from the holotype; G from *Almeda et al.* 6328.)

ing rounded-quadrate with age. Leaves of a pair equal or unequal in size (if unequal then the smaller one $\frac{2}{3}$ to $\frac{3}{5}$ the size of the larger one); petioles 1.5–7 cm long, sparsely to moderately lepidote when young; blades membranaceous, 8–25.4 cm long and 4.5–14 cm wide, elliptic to elliptic-obovate, apex acuminate, base acute, margin entire, 5-nerved or inconspicuously 5–7-plinerved with a prominulous network of secondary and higher order veins, glabrous above, sparsely and deciduously lepidote below. Inflorescence a terminal paniculiform dichasium 12–30 cm long on a well-defined arching or deflexed peduncle mostly 3.5–10 cm long, the rachis glabrous; bracteoles sessile, early deciduous, narrowly triangular to subulate, 0.5–1 mm long, 0.25–0.5 mm wide, sparingly lepidote to glabrate abaxially, margin entire. Pedicels 0.5–3 mm long, sparsely to moderately lepidote. Flower buds oblong-ellipsoid, 6–10 mm long 3.5–4.5 mm wide, sparsely to moderately lepidote basally, the calyptriform calyx 3–5 mm long, acuminate; torus glabrous adaxially and callose thickened along the adjacent circumscissile line. Petals 5, glabrous, obovate, reflexed to widely spreading, gently lobed to somewhat oblique apically, 5–6 mm long, 4–5(–6.5) mm wide distally. Stamens (8)–9–10; filaments glabrous, complanate, 2.5–3 mm long; anthers 2–3 mm long, 0.75 mm wide, pale yellow, linear-oblong with a ventrally inclined terminal pore 0.25 mm in diam.; connective thickened dorsally but not prolonged or appendaged at the filament insertion. Ovary (at anthesis) completely inferior, 6-celled, ovoid, the apex glabrous, smooth, and lacking an elevated cone or collar. Style conspicuously curved distally, glabrous, 3–4 mm long; stigma capitate, 0.75 mm in diameter, copiously papillose but lacking well-defined lobes. Berry purple at maturity, depressed-ovoid, 5–6 mm long and 5–7 mm in diameter. Seeds narrowly pyriform, 0.75 mm long, yellowish-white, irregularly muriculate on the convex face.

PHENOLOGY.—Flowering specimens have been collected in April, July, August, and September; specimens in young fruit have been collected in September, but mature fruiting collections have been made only in January.

DISTRIBUTION.—A local and uncommon understory tree of wet evergreen forests from southeastern Costa Rica (Limón) southeast to the Caribbean slopes of Panama, from Bocas del Toro province to Cerro Tute (Veraguas) and the region

north of El Copé (Coclé) from 90–1,200 m (Fig. 2).

ADDITIONAL SPECIMENS EXAMINED.—COSTA RICA. Limón: Hitoy Cerere Biological Reserve, SW of Valle La Estrella along Río Cerere to ca. 1 km upstream from Quebrada Barrera, 9°40'30"N, 83°02'W, 31 Jul. 1985, *Grayum & Hammel 5773* (CAS). PANAMA. Bocas del Toro: above Chiriquí Grande on a side road ca. 10 miles below the continental divide ca. 2½ miles E on that road, 8°55'N, 82°10'W, 19 Jan. 1989, *Almeda et al. 6328* (CAS, CR, MO, NY, PMA). Coclé: New Works, 7 km N of El Copé, 18 Aug. 1977, *Folsom 4938* (CAS, PMA); forest on continental divide above El Copé, 8°38'N, 80°38'W, 27–29 Apr. 1985, *Hammel 13663* (CAS). Veraguas: Cerro Tute, trail past agricultural school near Santa Fe, 17 Sep. 1979, *Antonio 1840* (CAS).

Specimens of *C. muriculata* were first collected in 1977 but the distinctiveness of this species became evident only after study of the flowering collection designated here as the type. The distinguishing features of *C. muriculata* are its quadrate carinate distal branchlets; sparingly lepidote indument on lower leaf surfaces, pedicels, and flower buds; distinctly pedunculate paniculiform dichasia; and muriculate seed coat. Collectors have described the petals of this species as deep blue (*Folsom 4938*), pale blue-violet (*Grayum & Hammel 5773*), lavender (*McPherson 12836*), and purple (*Antonio 1840*, *Hammel 13663*). All of these collectors, except Folsom and McPherson, have also noted that the inflorescence is pendant or deflexed. Because these characters are unusual in *Conostegia* and potentially diagnostic, additional field study is needed to determine whether they are consistent.

The close relatives of *C. muriculata* among described congeners are not readily apparent. It superficially resembles *C. tenuifolia* J. D. Smith and *C. rhodopetala* J. D. Smith. The former, described from Costa Rica (Smith 1899) but now also known from Nicaragua and Panama, differs in having narrower leaves (3.6–7.4 cm) with abruptly caudate-acuminate apices, ovoid buds that are conspicuously subtruncate at the base (when dry), 16–22 stamens per flower, an ovary with 10–12 locules, and seeds with a smooth testa. In having oblong-ellipsoid acuminate flower buds and a 6-celled ovary, *C. muriculata* is also similar to the Costa Rican endemic *C. rhodopetala*. In the field, *C. rhodopetala* is readily distinguished from other species of *Conostegia* by the bright pink coloration of inflorescence branches, flower buds, and petals. The most notable characters separating it from *C. muriculata*

include its sparse and deciduously stellulate-furfuraceous indument on the inflorescence rachis, longer petals (8–10 mm), larger number of stamens per flower (12–17), and smooth seeds.

The name for this species is the diminutive of *muricatus*, Latin for short and tubercular excrescences. It emphasizes the finely sculptured seeds. The seeds of *C. polyandra* Benth. are depicted as muriculate in the plate included with the protologue (Bentham 1844). However, an examination of several recent collections of *C. polyandra* from throughout its range reveals that its seeds are completely smooth.

***Conostegia orbeliana* Almeda, sp. nov.**

(Fig. 4)

TYPE.—PANAMA. Bocas del Toro: vicinity of Cerro Colorado mine above San Felix, along trails N of road along continental divide, 8°35'N, 81°50'W, 1,500 m 26 Jan. 1988, *McPherson 12014* (holotype: CAS!; isotypes: CR!, DUKE!, MEXU!, MO!, PMA!, TEX!, US!).

Arbor 6–7 m. Ramuli quadrangulati demum teretes sicut foliorum subtus venae primariae inflorescentia hypanthiaque dense pilis stellatis et pilis stipitato-stellatis induti. Petioli 1.2–3 cm longi; lamina 5–11.2 × 3–5.5 cm elliptica vel elliptico-ovata, apice acuminata vel cuspidata, basi acuta, 3–5-plinervata, membranacea et obscure serrulata vel subintegra. Inflorescentia 4–7(–10) cm longa laxa pauciflora; pedicellis (ad anthesim) 8–20 mm longis; bracteolis 1–2 mm longis mox caducis. Alabastra matura acuta vel acuminata 12–15 × 9–11 mm; calyx calyptriformis 6–8 mm longus. Petala 8, glabra, 11–15 × 9–13 mm, obovata apice rotundato vel rotundato-subtruncato. Stamina 19–22, isomorphica glabra; filamenta 5–5.5 mm longa; antherarum thecae 3–3.5 × 0.75 mm oblongae, poro dorsalter inclinato; connectivum nec prolongatum nec appendiculatum. Stylus 7 mm glaber, stigmatum subpeltato centro concavo costato; ovarium 12–13-loculare et omnino inferum, collo 2 mm alto glabro paulo costulato.

Trees 6–7 m tall. Uppermost internodes quadrate becoming rounded with age, moderately to copiously covered with a mixture of sessile-stellate and short stipitate-stellate hairs. Leaves of a pair equal to somewhat unequal in size; petioles 1.2–3 cm long; blades membranaceous, 5–11.2 cm long and 3–5.5 cm wide, elliptic to elliptico-ovate, apex acuminate to cuspidate, base acute, margin inconspicuously serrulate to subentire, 3–5-plinerved, the innermost pair of elevated primaries diverging from the median nerve in opposite or subalternate fashion 5–9 mm above the blade base, glabrous above at maturity, moderately covered with a mixture of sessile-stellate and short stalked-stellate hairs on the elevated primary and secondary veins below. Inflores-

cence a terminal paniculiform dichasium 4–7 (–10) cm long, the rachis copiously beset with sessile stellate and short stalked stellate hairs; bracteoles sessile, early deciduous, subulate to linear-oblong, 1–2 mm long, 0.25–0.5 mm wide with pubescence like that of the rachis on the abaxial surface, margin entire. Pedicels 8–20 mm long, copiously beset with sessile-stellate and short, stalked, stellate hairs. Flower buds ellipsoid, 12–15 mm long, 9–11 mm wide, coarsely verrucose for the basal half of their length and moderately covered with tardily deciduous stellate hairs throughout, the calyptriform calyx 6–8 mm long, acute to acuminate; torus glabrous adaxially. Petals 8, glabrous, connivent, white, obovate, widely spreading, apically rounded to subtruncate with irregularly lobed undulate margins, 11–15 mm long, 9–13 mm wide distally. Stamens 19–22, typically positioned in a ring around the style; filaments glabrous, complanate, 5–5.5 mm long; anthers 3–3.5 mm long, 0.75 mm wide, yellow, linear-oblong, truncate to broadly rounded at the apex with a somewhat dorsally inclined terminal pore 0.25 mm in diameter; anther connective thickened dorsally but not prolonged or appendaged at the filament insertion. Ovary (at anthesis) completely inferior, 12–13-celled, depressed-globose, the apex glabrous, gently fluted or costulate with an elevated stylar collar 2 mm long. Style straight, glabrous 7 mm long; stigma flared, subpeltate and crateriform with 12–13 longitudinal riblike lobes. Mature berry and seeds not seen.

PHENOLOGY.—The two known collections, both of which are in flower, were made in January.

DISTRIBUTION.—A local and uncommon element of cloud forest vegetation on slopes and valleys in the vicinity of Cerro Colorado mine above San Felix in western Panama at 1,450–1,500 m (Fig. 2).

ADDITIONAL SPECIMENS EXAMINED.—PANAMA. Bocas del Toro/Chiriquí Border: slopes and valleys of Cerro Colorado region, 27 Jan. 1989, *Almeda et al. 6445* (CAS, MO, NY, PMA).

Judging from the few specimens collected, this species, which was first gathered in 1988, is apparently rare and localized. *Conostegia orbeliana* has a combination of features that readily set it apart from its congeners. The uppermost cauline internodes, pedicels, and inflorescence rachis are mostly densely beset with a mixture of sessile

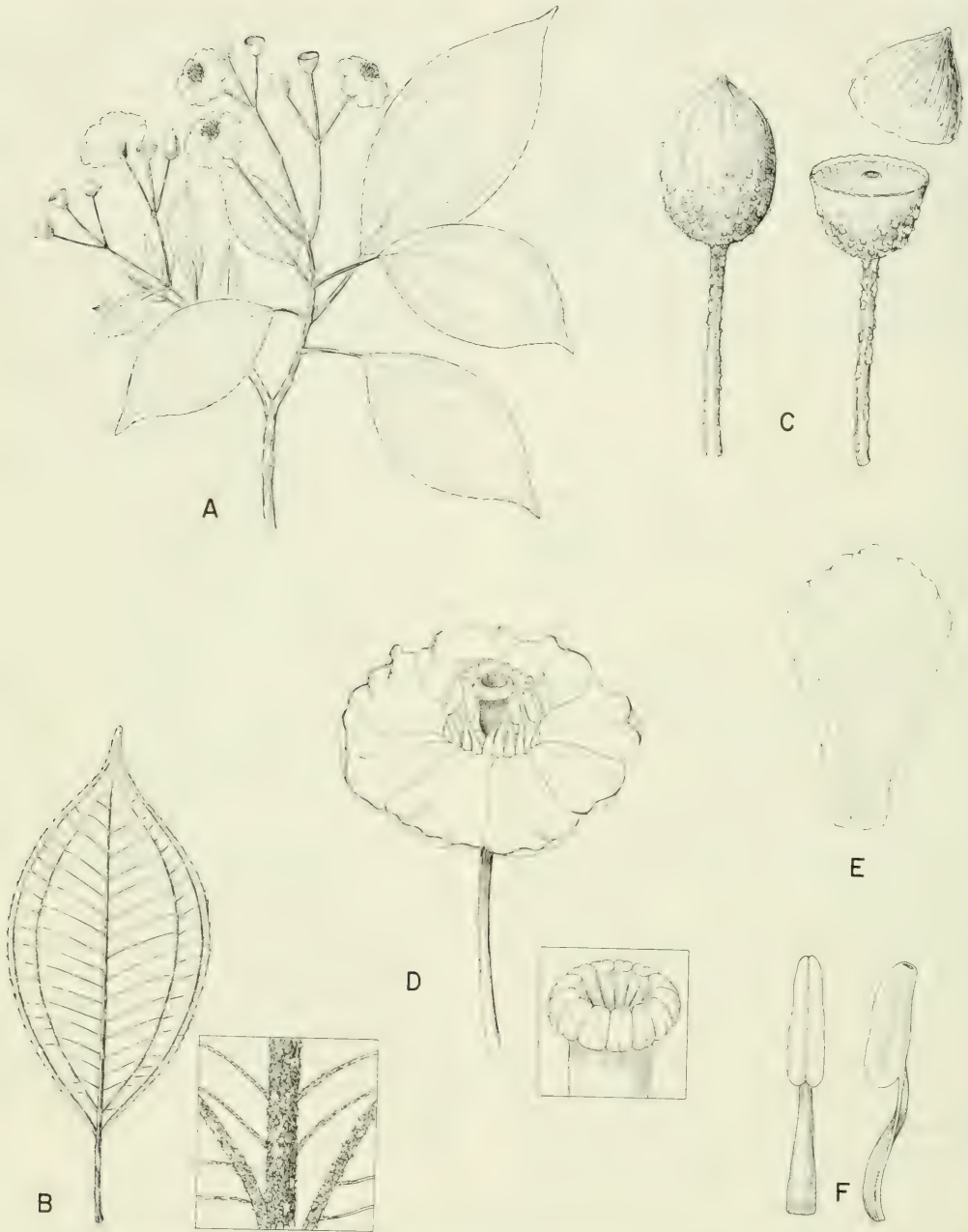


FIGURE 4. *Conostegia orbeliana* Almeda. A, habit, $\times$ ca. $\frac{1}{2}$; B, representative leaf (abaxial surface) with enlargement (right), $\times$ ca. $\frac{2}{3}$; C, flower bud (left) and bud with detached calyptiform calyx and floral parts removed (right), $\times$ ca. $1\frac{1}{2}$; D, representative flower showing spreading petals, straight style, and stigma enlargement (right), $\times$ ca. $\frac{1}{5}$; E, petals (adaxial surface), $\times$ 3; F, stamens, ventral view (left) and lateral view (right), $\times$ 6. (A–C from the holotype; D–F from Almeda *et al.* 6445.)

stellate and short-stalked stellate hairs. Its inconspicuously serrulate to subentire leaves are unusually small for a species with comparatively large flowers that measure ca. 3 cm in diameter.

Other notable features of *C. orbeliana* are the coarsely verrucose hypanthial cups (Fig. 4C) and the dorsally inclined anther pore (Fig. 4F).

Overlapping similarities in foliar pubescence,

petal and stamen numbers, style posture, stigma morphology, and the number of ovary cells suggest that *C. orbeliana* is closely related to *C. volcanalis* Standley & Steyererm. of southern Mexico (Chiapas, Guerrero, Jalisco), Guatemala, Honduras, and Nicaragua. I define *C. volcanalis* in a broad sense, perhaps too broadly, to accommodate what I interpret as regional variation in leaf and petal size, bud shape, and foliar pubescence density. Some populations, for example, have leaves that are nearly glabrous below. Others have lower leaf surfaces beset with a mixture of sessile stellate and long-stalked stellate hairs, whereas others have only long-stalked stellate hairs mostly confined to the elevated primary and secondary veins. Even in its broadest circumscription, *C. volcanalis* is readily separated from *C. orbeliana* by its larger (12–27 × 6–15 cm) mostly undulate-dentate leaves, longer petioles (3.5–6.7 cm), smaller floral buds (8–10 mm), and completely smooth pedicels and hypanthial cups.

This species is named for Orbelia R. Robinson, friend and fellow student of the Melastomataceae, in grateful recognition of all the volunteer technical and research assistance she has rendered in the herbarium of the California Academy of Sciences during the past decade.

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RESUMEN

Conostegia es un género natural de amplia distribución pero con gran concentración en Costa Rica y Panamá, 33 de sus 50 especies ocurren allí. La relativa inaccesibilidad a ciertas áreas tales como las selvas de la parte sur de Costa Rica (Limón) y de las provincias de Bocas del Toro y Chiriquí en Panamá, se reflejan en el número de especies recolectados hasta el presente. El número de los pétalos y estambres, la posición del estilo, la forma y tamaño del estigma, y el número de lóculos en el ovario son a menudo caracteres taxonómicos muy útiles en *Conostegia*. Se proveen descripciones, ilustraciones y discusiones referentes a las afinidades de tres especies nuevas: *Conostegia fragrantissima* y *C. orbeliana* de Panamá y *C. muriculata* de Costa Rica y Panamá. También se presenta un mapa de distribución para todas ellas.

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